Macrofossil Evidence for Quaternary Plant Extinction and Vegetation Change in Western Tasmania.

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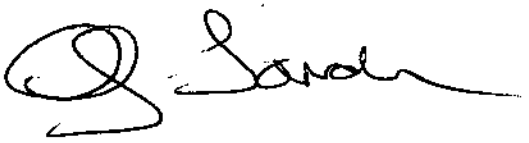
This thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any tertiary institution and, to the best of my knowledge and belief, it contains no material previously published or written by any other person, except when due reference is made in the text of the thesis.



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Abstract

Macrofossils from Pleistocene sediments in western Tasmania are investigated in order to reconstruct vegetation from this critical period in the history of Australia's vegetation. The microfossil record shows that many taxa, notably the common Tertiary taxa *Nothofagus* subgenus *Brassospora*, Araucariaceae, *Dacrycarpus* and *Dacrydium*, were present in western Tasmania during the Latest Pliocene or Earliest Pleistocene but are now extinct from Tasmania. Most of these taxa are likely to have been rainforest species, but some may have been from sclerophyll vegetation (e.g. *Beauprea*). A few of these persisted into the Early-Middle Pleistocene and only *Quintinia* to the Late Pleistocene.

Macrofossils of now globally and regionally extinct taxa occur in the Early-Middle Pleistocene Regatta Point sediments. Most of these extinct taxa are not distinct in the relatively good microfossil record of that area. Some clearly sclerophyllous taxa have become extinct e.g. *Banksia strahanensis* and *Oxylobium* sp. nov. Rainforest taxa no longer occurring in Tasmania have affinities with species from temperate New Zealand (e.g. *Quintinia* sp. nov.), montane north-eastern New South Wales and Queensland (e.g. *Rubus* cf. *moorei* forma *glabra*, aff. *Austromyrtus* and *Laurophyllum* sp.). Macrofossils of only one extinct species occur in sediments younger than Regatta Point : *Banksia kingii* from the Late Pleistocene Melaleuca Inlet sediments.

Local climatic and vegetation reconstructions for the times of deposition are made for the Regatta Point, the middle Pleistocene Regency and the late Pleistocene Melaleuca Inlet sediments based on floristics. Vegetation reconstructions include analysis of diversity using both floristics and a modified rarefaction method. Both climatic and vegetation reconstructions are interpreted in terms of taphonomic studies both in this work and elsewhere. Regression modelling of the leaf size of *N. cunninghamii* from modern forest floor litter against BIOCLIM synthetic climatic parameters indicates that leaf length is well correlated to temperature of the growing season, and palaeo-temperatures are estimated for the fossil floras.

The extinctions are interpreted in terms of the climatic and vegetation reconstructions of the sites, and broader scale knowledge of late Cenozoic climate, vegetation and glacial history. Many Tertiary taxa survived the climatic disruptions of the Early Pleistocene, but probably become extinct directly or indirectly due to the glaciations of the Middle Pleistocene. Rainforest diversity is lower now than during the Early Pleistocene, but the results are ambiguous for overall diversity. There is no reason to suspect that Tasmania could not support more diverse rainforest under modern conditions.

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Contents

Chapter 1 : Fossils and Palaeoecology

1.1 : Introduction

The fossil record can be used to study the relationships between past organisms and their environments (palaeoecology) through reconstructing past communities (elucidated in Birks and Birks 1980) or studying the relationships between the morphology of individual taxa (or of whole communities) and environmental factors. These studies are also capable of creating insight into the ecology of the modern world. This has recently received much attention and its literature has been reviewed and discussed by Schoonmaker and Foster (1991). In particular, palaeoecology provides evidence on a much longer time scale than any study in neoecology, which works on a time scale of at most a few decades. Therefore, palaeocological studies may allow detection of the effects of ecological factors and principles that are obscure in neoecology. These factors include climate, continental drift, extinction and evolution. An often cited example is the use of pollen records to show that communities tend to be collections of individually adapted organisms rather than groups of co-evolved organisms, and that community composition tends to change rapidly with environmental change (Bennett 1990). Adams and Woodward (1992) discuss the record of past environmental change, and the probable impacts of these changes on past communities, and suggest that this can help our understanding of the impact of future change.

Many (if not most) palaeoecological studies have focussed on the Late Pleistocene and Holocene (e.g. Huntley and Webb 1988), partly for technical reasons (good sites are more easily found, and these sites are often easily and reliably dated by ^{14}C methods) and partly for theoretical reasons (fossil taxa of these ages are more likely to have similar ecological preferences to their modern counterparts than older fossils, and more recent events are likely to have had a greater direct impact on current ecology than older events). A high proportion of these studies have been in the northern hemisphere. A diversity of methods have been employed in these palaeoecological studies, including associating tree rings with climate (e.g. Schweingruber 1988), tracing the proportions of pollen of major taxa over long periods from large areas (reviewed by Schoonmaker and Foster

1991), as well as vegetation and climate reconstructions based on floristics of mainly microfossils, but also macrofossils (e.g. Collinson and Scott 1987). A period which remains relatively neglected, particularly in Australasia, is the Early and Middle Pleistocene. In addition, macrofossils remain poorly studied in Australasia but offer much detail which is unavailable to other methods of palaeoecology (see below). Only a few Australian macrofossil floras have been examined in detail such as the Tertiary floras of the Latrobe Valley, Victoria, and some Oligocene floras of Tasmania.

This work, therefore, enters a relatively poorly studied and potentially fruitful field, Pleistocene macrofossils of western Tasmania. Several rich and interesting Pleistocene macrofossil sites are known in this area, and potentially many more exist. This thesis introduces a considerable amount of new data and provides a synthesis of the known Pleistocene macrofossil record of western Tasmania. In particular, it demonstrates the presence of macrofossils in Pleistocene sediments in Tasmania of now locally and/or globally extinct plant taxa. Implications (including changes in the diversity and species composition of plant communities) and possible causes of these extinctions are considered. Detailed study of leaf size of fossil and extant *Nothofagus cunninghamii* * indicates changes in diversity and community composition not previously recognised. The fossil taxa are illustrated and described taxonomically where necessary.

1.2 : Macro- and Microfossils : The Nature of the Evidence

The history of plant extinctions and community change is restricted by the nature of the evidence. Extinctions and past vegetation may be inferred from the fossil record. The fossil record is notoriously incomplete, but to some extent this incompleteness is predictable. Most Quaternary vegetation studies have been based on microfossil (pollen and spores) evidence, mainly because sediments containing well preserved microfossils are more frequent than sediments with well preserved macrofossils, and because of the widespread acceptance and understanding of palynology due its use in

* (Taxonomic authorities for *N. cunninghamii* and all other species cited in this thesis are listed in Appendix 1.)

mining geology. Macrofossils (foliar matter with or without well preserved cuticles, flowers, fruit and wood) have been less well studied. They are often undatable without a corresponding pollen flora.

Readily identifiable microfossils occur in many Quaternary sediments. At present microfossils may be identified to varying degrees of resolution : some are identifiable to species, many to genus but many others only to subfamily, family or groups of families. Many extinct species are, therefore, likely to have produced pollen which is placed in extant taxa and their extinction would not be apparent in the microfossil record. Microfossils are often used to infer the local and regional vegetation of sites at the time of deposition, since many pollen types are abundant, wind dispersed and well preserved (Birks and Birks 1980). Estimates of the abundance of vegetation types can be made using the proportions of representative microfossil types, providing that the differences in dispersal distances, the quality of preservation and the abundance of production of the pollen and spore types are taken into account. The contribution of water transported palynomorphs may, however, be considerably higher than that of aerially transported palynomorphs with the result that palynomorph assemblages may be strongly biased towards riparian vegetation, with poor representation of other vegetation. The relative contribution of taxa to sediments and the bias toward riparian vegetation varies from taxon to taxon with differences in the production and effectiveness of wind transport of their palynomorphs (Birks and Birks 1980).

Organically preserved macrofossils generally have higher information content than microfossils and can often be identified to more precise taxonomic levels. Extinct taxa which are obscure in the microfossil record may therefore be apparent in the macrofossil record. Ecological information can also be extracted from macrofossils (e.g. the leaf morphology and anatomy vary with climate and soils both within and between taxa, and climatic information can be derived from isotope analysis of tree rings). Macrofossils are poorly dispersed and some taxa and types of organ are much more likely to be preserved than others (see Chapter 4). Sediments containing well preserved macrofossils are relatively uncommon. Macrofossils, therefore, offer higher geographic resolution than microfossils and hence can show local vegetation and vegetation changes, but produce a very incomplete record of vegetation change and extinction both in time and in space.

In addition, there are some biases imposed by past palaeobotanical practices. In some parts of the world it has been common practice to assign Quaternary fossils to extant species, and earlier fossils to extinct species

virtually regardless of the strength of affinity with extant species. Other workers have tended to assign fossils to form genera regardless of age and probable taxonomic affinity. The use of a form genus rather than a living genus tends to obscure our understanding of palaeoecology (Collinson 1986) provided there is considerable evidence to include the fossil(s) in the living genus.

Chapter 2 : General Methods

2.1 : The Study Area

This study is based on fossil deposits in an area of western and southern Tasmania shown in Figure 2.1, and comparisons with extant vegetation are centred on this area, although comparisons are also made with extant vegetation of the rest of the south Pacific, and south-east Asia. For convenience the study area will be referred to as western Tasmania from here on. This division of Tasmania into a western province and an eastern province is not arbitrary. It represents a division of the island into an area of pre-Carboniferous base geology with high rainfall and mainly infertile soils (west) and an area of Permian to Recent base geology mainly with more fertile soils and lower rainfall. A corresponding major division is recognisable in vegetation and the distributions of most terrestrial and freshwater plant and animal groups (Reid *et al.* in press).

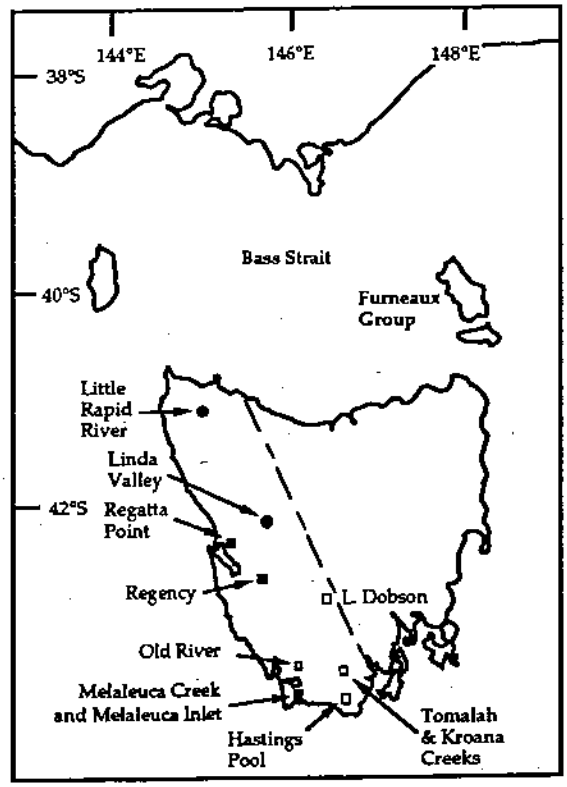


Figure 2.1 : The study area (west of the broken line in Tasmania). Location of fossil and extant sites. Closed squares are Quaternary fossil deposits, closed circles are Tertiary fossil deposits and open squares are modern taphonomic sites.

2.1.1 : The Modern Environment of Western Tasmania

Western and southern Tasmania is an area with a perhumid cool climate (Gentilli 1972) (Table 2.1) rugged topography, and varied geology. The geology is primarily pre-Carboniferous, with large areas of Cambrian and Precambrian metamorphics, but also igneous and sedimentary rocks. Quaternary sediments are widespread, mainly in high altitude areas and river valleys. The pre-Carboniferous areas generally produce highly infertile soils, and most of the Quaternary sediments are also infertile, being reworking of the infertile pre-Carboniferous rocks. Some parts of the northern half of western Tasmania have significant amounts of Tertiary basalts, which produce much more fertile soils. The Strahan Sub-basin is exceptional, being a large area of Tertiary sediments (Department of Mines, Tasmania 1976).

Site	Latitude (°S)	Longitude (°E)	Altitude (m)	Mean temperatures (°C)				Mean precipitation		
				Annual	Daily range	Coldest quarter	Warmest quarter	Annual	Wettest month	Driest month
Regatta Point	42° 9'	143° 20'	10	11.6	9.6	8	15.4	1620	179 July	77 Feb.
Regency	42°10'	143° 38'	180	10.8	9.3	7.1	14.8	2812	318 July	126 Feb.
Old River	43° 19'	146°14'	10	11.5	8.8	8.1	15	1973	205 May	106 Feb.
Melaleuca Inlet	43° 26'	146° 9'	10	"	"	"	"	"	"	"
Melaleuca Cr.	43° 25'	146° 9'	10	"	"	"	"	"	"	"
Lake Dobson	42° 41'	145° 35'	1150	5.7	7	1.6	10.6	1553	151 May	90 Feb.
Hastings Pool	42° 22'	146° 5'	390	9.3	9	5.7	13.2	1495	171 July	77 Feb.

Table 2.1 : Location and some climatic details of the major fossil and extant sites. Climatic variables are derived from BIOCLIM (e.g. Busby 1988).

Jackson (1965) described the extant lowland vegetation of southern and western Tasmania as a mosaic of hummock sedgeland, shrub moor, wet scrub, wet sclerophyll forest, mixed forest and rainforest communities (dominated by *Nothofagus cunninghamii*, *Atherosperma moschatum* and *Eucryphia lucida*). ~~communities.~~ More recently, the hummock sedgeland and shrub moor communities have been classified together as 'sedgeland-heaths' by Jarman and Crowden (1978). Fire frequencies are now high in sedgeland -heath and wet scrub communities in Tasmania (Jackson 1965; Brown and Podger 1982), although there remains controversy as to whether the

distribution of these communities is determined principally by fire history or by edaphic features (Jackson 1968; Mount 1979; Brown and Podger 1982).

Above about 300 m a.s.l. in the south and 600 m in the north the lowland vegetation grades more or less continuously into subalpine at about 500 m in the south and about 800 m in the north, and then into alpine vegetation at about 800 m in the far south and about 1200 m in the north. These altitudes vary with aspect. In well drained areas of low fire frequency this gradient involves a transition of rainforest types, with increasing proportions of conifers, particularly *Athrotaxis* species from about 300 m to about 1400 m a.s.l., and *Diselma archeri* in the subalpine and alpine zones, and *Microcachrys tetragona* in the alpine areas. *Nothofagus gunnii* is common in the subalpine and low alpine areas. The diversity of the rainforest tends to increase with increasing altitude. In areas of moderate fire frequency the altitudinal transition is from sclerophyllous forest through sclerophyllous montane woodland to alpine shrubberies. The Epacridaceae, Asteraceae, Proteaceae and Myrtaceae are prominent in these subalpine vegetation types. Tree lines tend to be poorly defined, and alpine herbfields are prominent only in areas of poor drainage and/or long snow lie (Crowden in press). The poorly defined tree line occurs at altitudes from about 750 m in far southern Tasmania, to about 1200 m in north -western Tasmania (Kirkpatrick 1982).

Large areas of western Tasmania up to 900 m with particularly high fire frequency, depauperate soils and often poor drainage are occupied by sedgeland-heath up to about 2 m tall dominated by sedges, particularly *Gymnoschoenus sphaerocephalus* (Cyperaceae), and also other Cyperaceae and Restionaceae, and myrtaceous (*Melaleuca* spp. and *Leptospermum* spp.) and epacridaceous shrubs (*Sprengelia incarnata* and *Epacris* spp.) (Brown in press). Interspersed with this vegetation in areas of somewhat lower fire frequencies, particularly following watercourses, are areas of wet scrub up to about 15 m tall, usually dominated by *Eucalyptus nitida* or *Leptospermum* spp., and containing Myrtaceae, Epacridaceae and *Acacia* shrubs.

The coastal vegetation of western Tasmania is composed mainly of a flora particularly adapted to high winds, salt spray and depauperate

siliceous substrates. This vegetation is floristically distinct from non-coastal lowland vegetation (Kirkpatrick and Harris in press).

2.1.2 : Environmental change in Tasmania during the Quaternary

Dramatic changes in climate and landform occurred in Tasmania during the Quaternary and these must have forced major changes in the vegetation of the western half. Kirkpatrick and Brown (1984 a) suggest that the initial glacial/interglacial cycles must have caused considerable extinction and speciation. Glaciations of higher areas occurred when the climate was significantly cooler than it is now, and than it was during most of the Tertiary.

There is geomorphological evidence for at least three, and probably four glaciations in western Tasmania. These glaciations are known as the Linda Glaciation (before 730,000 B.P.), the Moore Glaciation (probably some period between 730,000 and 390,000 B.P.), the Henty or Comstock Glaciation (before 130,000 B.P.) and the Margaret Glaciation (from before 48,000 B.P. to about 13,000 B.P.) (Fitzsimons and Colhoun 1991). The Linda Glaciation was the most extensive. The occurrence of the Moore Glaciation is uncertain, since it is dependant on the dating of the Regency Formation (see below). Since the action of glaciers often removes sediments laid down during previous glaciations it is possible that other less extensive glaciations have occurred leaving little or no apparent evidence.

Oxygen isotope ratios of Foraminifera from deep sea sediments give more direct evidence of climate change during the Cainozoic. The proportion of ^{18}O to ^{16}O (expressed as $\delta^{18}O$) in sea water is considered to be a climatic indicator. $\delta^{18}O$ of oceanic water increases as water temperature decreases, and as ice volume increases (which indirectly implies low temperatures). The Northern and Southern Hemispheres appear to respond, at least partly, independently. The calcareous microfossils of Foraminifera are believed to show the $\delta^{18}O$ extant at the time of the life of the organisms (Shackleton 1982). Records show that the $\delta^{18}O$ of deep sea Foraminifera have followed roughly cyclic variation over the last 7 million years with a general trend to higher proportions of ^{18}O and increasing magnitude of fluctuations, and most periods since the Late Pliocene having higher proportions of ^{18}O than during the Holocene (see Figure 2.2). There have been at least six periods in the last 800,000 years with much elevated proportions of ^{18}O (Shackleton and Opdyke 1973). It has been proposed that before the Late Pliocene most of the variation in

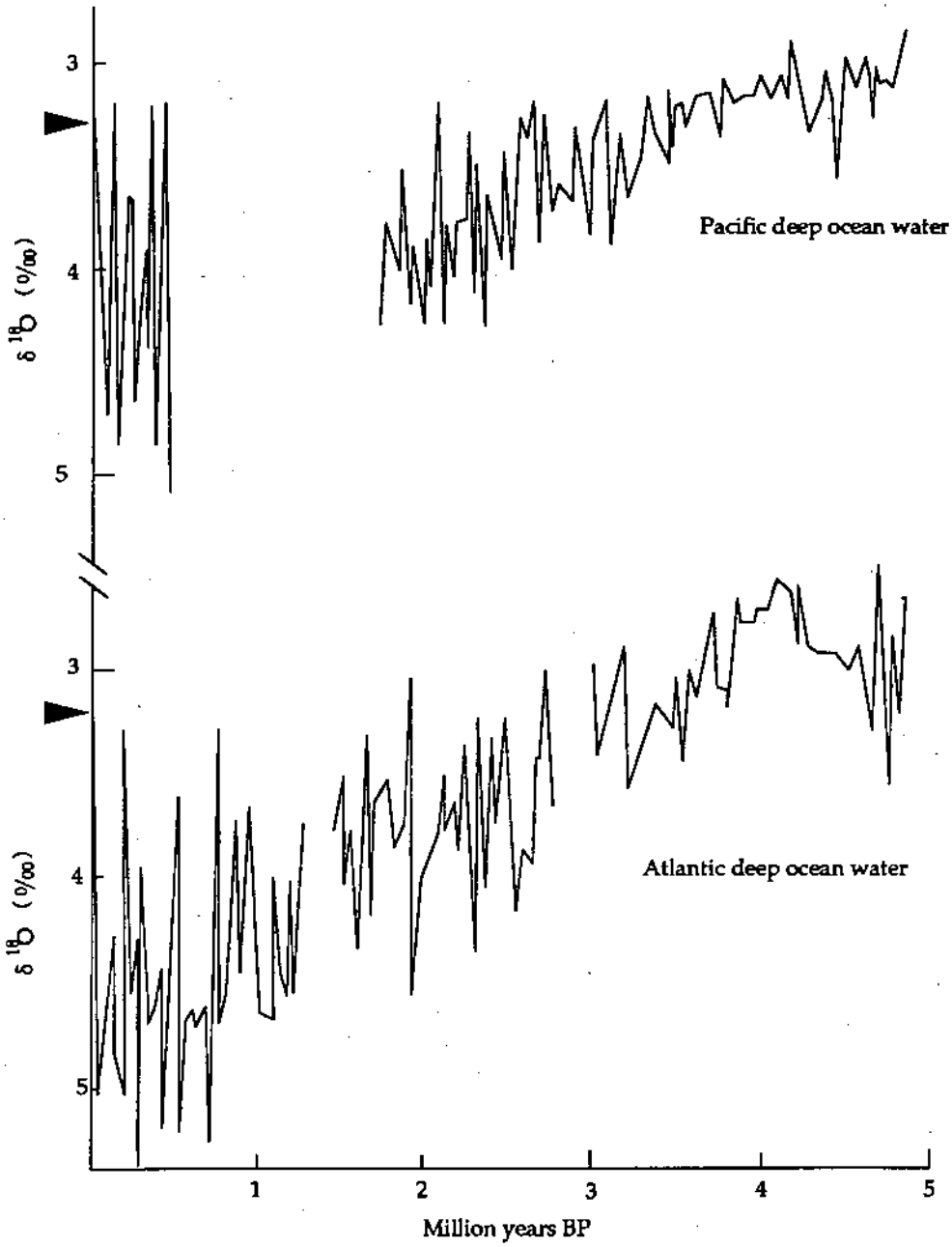


Figure 2.2 : Oxygen isotope curves (redrafted from Shackleton 1982) for the past 5 million years. The upper curve is for Pacific deep ocean water which probably gives a reasonable overall estimate of southen hemisphere conditions. The lower curve is for Atlantic deep ocean water which gives a more complete record for the last 2 million years, but southern hemisphere conditions probably followed the trends shown by the Atlantic deep ocean water less closely. The arrows indicate modern levels of oxygen isotopes.

$\delta^{18}O$ was the result of changes in sea temperature, and that the polar ice caps have become large since the Late Pliocene, and therefore the fluctuations in $\delta^{18}O$ are largely the result of changes in ice volume (Shackleton 1982).

There have, therefore, been many periods since the Late Pliocene which were cooler and/or more glaciated than at present. The glaciations probably became more severe during the Pleistocene, and conditions as warm as at present probably only occupied short periods during the Pleistocene. Variations in the Earth's orbit around the sun seem to have generated these cycles, with probable feedback interactions with ice volume, sea temperature, atmospheric CO_2 concentration and other factors (Berger 1978). Atmospheric CO_2 varied with temperature changes, with low CO_2 concentrations during colder periods and higher concentrations during warmer periods (Bartlein and Prentice 1989). Rapid warming occurred at the end of the glacials with most of the range from maximum cold to maximum warmth occurring in less than 10,000 years but the cooling phase between interglacial and glacial periods was slower (over periods of tens of thousands of years) (Bartlein and Prentice 1989).

Sea levels have also varied during the Pleistocene. Shackleton and Opdyke (1973) inferred that increased polar ice volumes and reduced temperature would lower sea levels, and, therefore, that the fluctuations in $\delta^{18}O$ were associated with changes in sea level. Chappell (1983) used the locations of limestone shelves on a shelf which has been tectonically continuously rising to infer periods of altered sea levels near New Guinea over the last 300,000 years. Cann *et al.* (1988) inferred the presence of lower sea levels over the last 50,000 years based on the presence of shallow water benthic foraminifera in tectonically steady marine sediments off southern Australia. These sources do not agree on the magnitude of sea level changes, but give reasonable agreement on their timing. However, it is clear that sea levels were low enough for continuous land to be exposed across Bass Strait for several periods during the Middle and Late Pleistocene and also possibly in the Early Pleistocene (Blom 1988). One of the later land bridges is likely to have provided the avenue through which Aboriginal man first entered Tasmania more than 30,000 years ago (Cosgrove 1989).

It is likely that the climate was drier than at present during cooler periods (Bowler 1982), although this difference may have been more marked in eastern and northern Tasmania than in the south and west (Sigleo and Colhoun 1981). To survive these cold arid conditions plant species would have needed either to have sufficiently wide tolerances to

continue at the same sites, or to have sufficiently rapid dispersal to migrate to new areas with conditions within their range of tolerance. A few taxa may have been able to evolve quickly enough to adapt to the rapidly changing conditions, but since most of the Pleistocene has apparently been cold, the rapid entry into the warm conditions of interglacials is likely to have placed stress on these taxa. Because of the rugged topography of western Tasmania many species would have found suitable temperature regimes nearby, however the increased aridity of the glacial periods may have posed major problems for many species.

The occurrence of land bridges is likely to have corresponded with the coldest and driest periods of the Pleistocene. Hope (1978) showed the existence of cold steppe on Hunter Island, now in south-western Bass Strait, during the colder part of the Last Glacial. This vegetation contained high proportions of grasses and Asteraceae shrubs and some chenopods. *Eucalyptus* and other tree taxa were rare. There was no evidence for any rainforest taxa. He inferred, based on this site and others in north west Tasmania that during the cooler periods of the Last Glacial large areas of the then Bassian Plain were semi-arid, and supported little forest. Bowler (1982) argued that reduction in temperature and increase in polar ice volumes produce increased aridity, especially in southern Australia. These are the conditions which also reduce sea levels. It is likely, therefore, that the Bassian Plain was relatively dry whenever it was in existence. There is evidence of cycles of aridity throughout the Pleistocene. Singh and Geissler (1985) showed cycles of vegetation change from apparently dry to wetter adapted floras in the Lake George, New South Wales, core. These cycles almost certainly corresponded to glacial/interglacial cycles through the Middle and Late Pleistocene. This core extends back through the Early Pleistocene where gaps occur which Singh and Geissler attribute to relatively arid periods when the Lake was dry. It is highly unlikely, therefore, that an effective migration route allowing the movement of rainforest and other mesic plant groups from mainland Australia to Tasmania and *vice versa* existed during the coldest parts of the Pleistocene. Land bridges may have persisted into warmer periods when polar ice was melting. Conditions suited to more mesic taxa than during the glacials may have existed in parts of the Bassian Plain under these circumstances. These periods are likely to have been of very short duration since the oxygen isotope record indicates very rapid transition from cold to warm conditions (e.g. in Tasmania the Last Glacial maximum was about 17,000 B.P. and full interglacial conditions were achieved by 10,000 B.P. (Fitzsimons and Colhoun 1991)).

The land bridge would have been most persistent through the

Furneaux Group in eastern Bass Strait (e.g. the reconstruction in Hope 1978). This area has relatively diverse topography, creating mesic microclimates in parts even during conditions drier than at present. All other areas of the Bassian Plain would have had low topography and therefore little microclimate differentiation. Rainforest now occurs both south (on north-eastern Tasmania) and north (on Wilson's Promontory) of the Furneaux Group. The eastern part of the Bassian Plain, from Wilson's Promontory through the Furneaux Group to north-eastern Tasmania, is likely to have been the best migration route for mesic taxa. Some rainforest taxa have been recorded from King Island, but land connections from King Island to mainland Australia are likely to have occurred only under the lowest of sea levels.

The current distribution of rainforest taxa in Tasmania suggests that the Furneaux Group may have provided a corridor only for the most hardy of rainforest species. The rainforests of north-eastern Tasmania are species poor compared with those of western and southern Tasmania. Notably, *Eucryphia*, *Acradenia* and *Anopterus* all occur in the wet forests of eastern Australia and western Tasmania, but not in north-eastern Tasmania, although edaphic and climatic conditions apparently suited to each of these species occur there. The rainforest patches now present on the Furneaux Group are even more species poor. This current species poverty may be evidence of the unsuitablity of the land bridge for most mesic taxa. Macphail (1979) argued that lowland rainforest is unlikely to have persisted in north-eastern Tasmania during the Last Glacial maximum, since pollen records from eastern Tasmania show little evidence of forest. *Nothofagus cunninghamii* almost certainly persisted in north-eastern Tasmania, however, since it is poorly dispersed and the dry graben of the midlands separates this area from the rest of Tasmania. It may have occurred as a sub-alpine shrub.

Fires apparently played a more significant role in the Late Pleistocene and Holocene than in the Early and Middle Pleistocene and may have been the cause of the species poverty of rainforests in north-eastern Tasmania, and in the Furneaux Group. Pollen studies from suitable sites from north-eastern Tasmania and the Furneaux Group would help resolve this problem.

Study of the microfossil record of western Tasmania has concentrated on the Late Pleistocene, particularly late Last Glacial and Holocene (e.g. Hope 1978; Colhoun 1978; Macphail 1979, 1984, 1986; Macphail and Colhoun 1985; Colhoun and van der Geer 1986; Colhoun 1988). There have been several studies from earlier in the Pleistocene, but

most of these have poor control on their ages (see below). An exception is the long core from Darwin Crater which provides an almost continuous record from about 700,000 B.P. to about 30,000 B.P. (See below). Colhoun (1988) described the top 20 m of the 60 m core. This records five cycles of vegetation change which can be attributed to glacial-interglacial cycles. The remainder of the core is unpublished (E. A. Colhoun pers. comm. and M. K. Macphail pers. comm.). Several other sites from interglacials and interstadials are known (Colhoun and Goede 1979; Colhoun 1980; Hill and Macphail 1985; Colhoun 1988; Fitzsimons *et al.* 1990; Jordan *et al.* 1991 - appendix 2) and one from a glacial (Colhoun and van der Geer 1987). Colhoun *et al.* (1989) showed a glacial-interglacial-glacial sequence.

These studies indicated some general trends. These mainly lowland pollen records were dominated during glacials by either *Nothofagus cunninghamii*/alpine coniferous shrubland (apparently under low fire frequency regimes), Asteraceae/Poaceae herbs (under the coldest, driest conditions) or sclerophyll woodland. Vegetation during interglacials was generally dominated by forest. Most of the interglacial sites show the presence of vegetation dominated by some combination of *Nothofagus cunninghamii*, *Lagarostrobos franklinii* and/or Casuarinaceae. Change from sclerophyll vegetation dominated by Casuarinaceae through to rainforest was common during the early parts of interglacials. *Eucalyptus* dominated interglacial vegetation has only been common during the Holocene, although eucalypts were a common feature of interstadial vegetation. The Casuarinaceae frequently formed a considerably higher proportion of pollen records before the Last Glacial than in modern vegetation. Widespread rainforest dominated by 'Tertiary' taxa (notably podocarpaceous conifers and *Nothofagus* subgenus *Brassospora*) declined during the Late Tertiary and was generally replaced by sclerophyll vegetation by the beginning of the Pleistocene in mainland southeastern Australia (Kershaw *et al.* 1991) . Casuarinaceae pollen dominated many mainland southeastern sites during interglacials, with *Eucalyptus* reaching present levels only in the Holocene (Kershaw *et al.* 1991) .

Low levels of charcoal occur in sediments in western Tasmania from early in the Quaternary e.g. in Regency (Fitzsimons *et al.* 1990), and in the alpine flora from Rosebery Mine which is probably of penultimate glaciation age (Colhoun and van der Geer 1987). However, significant amounts of charcoal occur in the Langdon River deposit, which is Last Interglacial or older (Colhoun *et al.* 1989), and in most of the upper 20 m of the Darwin Crater core (Colhoun 1988) and high levels existed during the last glacial at Ooze Lake (Macphail and Colhoun 1985). Charcoal levels are consistently

higher during glacial and interstadial periods than during interglacial periods in the Darwin Crater Core (Colhoun 1988, M. K. Macphail pers. comm.). Similarly, burnt macrofossils of the fire sensitive rainforest species *Athrotaxis cupressoides* and of more fire adapted species have been found from a deposit at Newton Creek which is at least 50,000 years old (R. S. Hill unpubl.). Hence, in summary, there is fossil evidence of fire throughout the Quaternary, mostly in sedgeland/sclerophyll communities, but also in rainforest, and fire has apparently been common at least since the Last Interglacial. Jackson (1965) proposed that raised fire frequencies were associated with human activity, and the fossil record is consistent with this hypothesis, although the increase in charcoal occurs before the earliest known record of human occupation, which is 30,000 B.P. (Cosgrove 1989).

2.2 : Fossil Sites

Pleistocene macrofossil-bearing sediments from three sites were studied : Regatta Point, Regency and Melaleuca Inlet (Figure 2.1). Some details of the location and current climate of these sites are given in Table 2.1. The microfossil assemblages in the Linda Valley sediments described by M. K. Macphail (Hill and Macphail in press) are also considered. The fossil assemblage found in the Melaleuca Inlet sediments has been described in Jordan *et al.* (1991), and parts of this work have been incorporated in this thesis. Macrofossil studies have been previously published for each site (Hill and Macphail (1985) for Regatta Point; Fitzsimons *et al.* (1990) for Regency and Jordan *et al.* (1991) for Melaleuca Inlet) but this work includes a detailed reassessment of the fossils from the first two sites (both those previously described and newly extracted ones). (The work published from the Melaleuca Inlet sediments was undertaken as part of my Ph.D. studies.) The sites were chosen because well preserved, fossil rich material was available for study, and they represent a wide time period in the Pleistocene. Macrofossils from Langdon River were discussed by Colhoun *et al.* (1989), and these were also reassessed, but are not discussed further here since little new information was obtained. There are other published accounts of macrofossil-bearing Pleistocene sediments from Tasmania, but these are all likely to be Late Pleistocene, and either they have been adequately described, or the material was not available for reinspection.

2.2.1 : Regatta Point (RPU1 & RPU2)

Quaternary sediments composed of irregular, rounded gravels containing occasional, large, soft mudstone clasts up to about 0.5 m^3 in volume overlie fossiliferous Eocene sediments at Regatta Point (see Figure 1 in Hill and Macphail 1985). These mudstone clasts occur in small-medium gravels near the base of the Quaternary sediments. Imbricated coarse gravels indicating a local river flow towards the north-west overlie the small medium gravels. These are underlain by bedded silts, and finally gravels and peat of possibly Late Pleistocene or Holocene age. The coarse gravels were likely to have been laid down by a high energy system, since they contain cobbles of up to 20 cm diameter. Hill and Macphail (1985) suggest that the sediments are glacial outwash gravels. The river may have been the ancestor of the King River (Figure 2.3), which now flows into Macquarie Harbour 4.5 km to the south-east, or it may have been a more local river.

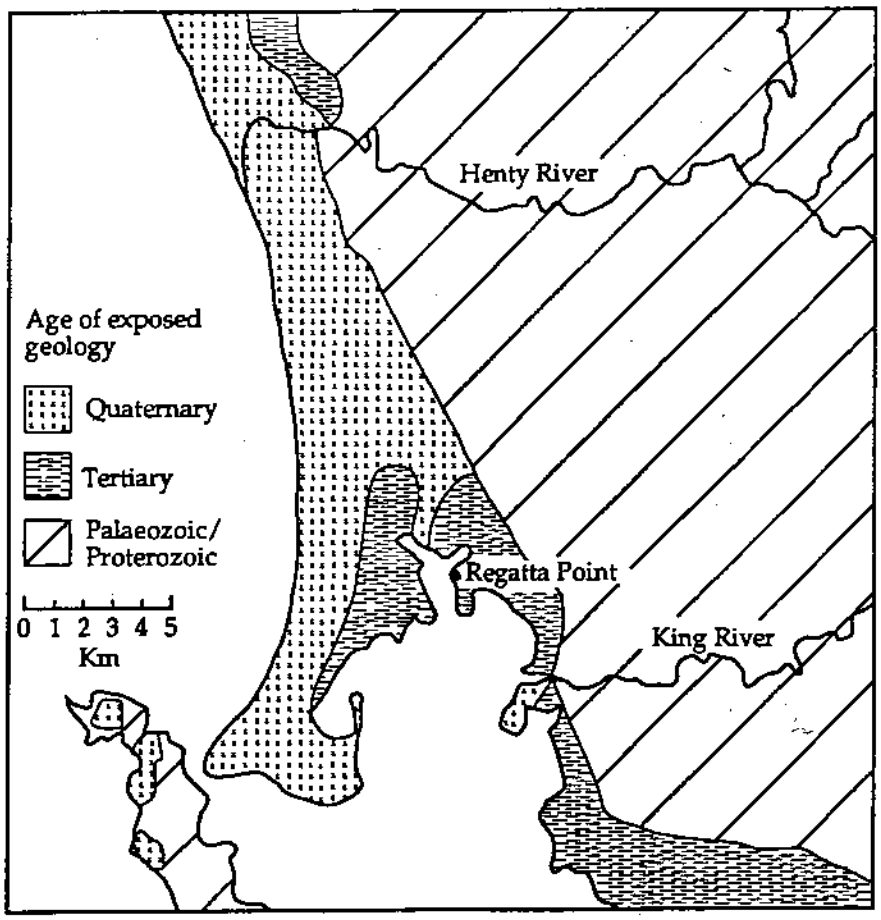


Figure 2.3 : Local geology of the Regatta Point area. Derived from Baillie *et al.*(1977).

The macrofossils are contained in the mudstone clasts. The mudstone blocks are angular and fragile, so an explanation of their presence in apparently high energy sediments is necessary. There is no obvious source for these clasts nearby, although there are sands of the same palynostratigraphic age 250 m north-west of this site, and elsewhere in the region (M. K. Macphail pers. comm.). Hill and Macphail (1985) proposed that erosion of sediments upstream released large mudstone blocks which were rafted downstream, perhaps by floating vegetation mats. An alternative hypothesis is that they were derived from sediments adjacent to the bank, and slumped into the river and mixed with the sediments there. A significant difference between these two hypotheses is that rafting allows for some significant transport of the blocks, whereas the other hypothesis implies that they have moved no more than a few metres.

There appears to have been some reworking of microfossils (Hill and Macphail 1985). Reworking of macrofossils is generally rare and is particularly unlikely to have occurred here, since many of the taxa which are most likely to be older than Pleistocene (i.e. those that are now extinct, and have affinities with taxa known to be common in the Tertiary) have large, apparently fragile, well preserved leaves. Leaves such as those of *Laurophyllum* are very unlikely to survive any reworking. The only possible exception is aff. *Dacrycarpus/Dacrydium*, which has small leafy stems which are poorly preserved and rare in the sediments. Podocarps, such as aff. *Dacrycarpus/Dacrydium*, usually have robust foliage, and are common in fossil bearing Cainozoic sediments in Tasmania. This taxon is not known, however, from the Regatta Point Eocene sediments.

The Regatta Point Upper sediments will be treated in two sections in this work : the fossils extracted from one very rich clast will be referred to as RPU2, and the fossils derived from several other separate clasts will be referred to as RPU1.

The block yielding the RPU2 assemblage has three distinct layers which are densely fossiliferous. Each of these layers is less than 1 cm thick and composed almost entirely of very well preserved leaves associated with little inorganic sediment. These layers are separated by thicker regions which are mainly inorganic sediment with varying proportions of fossils.

Each of the leaf-rich layers is likely to have been the result of a short period of sedimentation, and possibly a single flood event, since they are very well preserved and sedimentation would need to have been rapid enough to cover the plant material and so avoid decay. Also the layers contain well preserved stems of the mosses *Ptychomnion aciculare* and *Thuidium* sp. which are robust terrestrial wet forest mosses not normally found in streamways. Since these taxa do not have deciduous shoots their stems are likely to enter waterways primarily under flood conditions.

The blocks yielding RPU1 are less densely fossiliferous, and their stratigraphy is obscure in the field. The fossil assemblages from the different blocks comprising RPU1 contain similar species but differ in proportions of the species, whereas there are significant differences in species composition from RPU2. Therefore, all these floras are treated together as RPU1, even though they may have been derived from a range of periods.

The presence of low numbers of well preserved reworked marine dinocysts and spores and pollen which are diagnostic of the Early Eocene marine claystones of the Strahan Sub-basin indicate that the RPU2 sediments were initially deposited in this sub-basin (M. K. Macphail pers. comm.). Furthermore, low but persistent quantities of Chenopodiaceae pollen indicate that estuarine conditions were present near the site of deposition of the sediments (M. K. Macphail pers. comm.). Figure 2.3 shows the location of the site and the distribution of Quaternary sediments, the Tertiary sediments of the Strahan Sub-basin and the remaining Palaeozoic and Proterozoic rocks.

The RPU1 and RPU2 blocks are most likely to be sediments of different age from the same site which were moved and redeposited by the same event. The only way that they could be from different locations is if they were rafted. Rafting events such as this are highly unusual, so it is very unlikely that two such events occurred and deposited the blocks in the same area.

No area within 22 km of Regatta Point is over 800 m altitude or currently carries alpine vegetation. No point within 11 km of the current extent of the Strahan Sub-basin between the King River and the Henty River is over 350 m altitude. The intervening area is primarily composed of

hard pre-Carboniferous rocks which have not been glaciated except for a tongue of ice down the King Gorge (E. A. Colhoun pers. comm.) (Figure 2.3). There has been relatively little uplift in this area since the Jurassic (Ollier 1986). Hence, it is highly unlikely that any area within 11 km of the site of deposition would have been more than 400 m above the site of deposition of the mudstones. Relatively little range in climate was likely within the region at any one time. It is unlikely, therefore, that leaves derived from high altitude vegetation would have enterred the sediments.

2.2.2 : Regency (RE)

Macrofossils were extracted from a vertical core through richly organic material at the Regency site. This core is the same one used by Fitzsimons *et al.* (1990) to describe the Regency Formation. The organic deposit consists of peat interspersed with silty layers, and is likely to have been a backswamp of a river (Fitzsimons *et al.* 1990). This fossil assemblage will be referred to in places as RE, and substrata will be referred to according to their depth in the core.

2.2.3 : Melaleuca Inlet (ME)

Sediment containing macrofossils was collected from the late C. D. (Denny) King's tin mine at Melaleuca Inlet, south-west Tasmania (Figure 1 in Jordan *et al* (1991) Appendix 2). The lens was found amongst coarse sand and gravels at a depth of approximately 2.5 m. The abundance of coarse organic material and the large siliceous particle sizes suggest a high energy depositional environment such as an eddy pool or levee overflow along a fast flowing river. The lens was entirely excavated in mining work about 20 years ago, but all the fossiliferous sediment was piled up and left, without addition of other material (C. D. King, personal communication). Only consolidated sediment was collected for this work, and hence the material is unlikely to be contaminated, except for impregnation by humic water.

The fossil assemblage from Melaleuca Inlet will be referred to as ME from here on. The modern vegetation of the Melaleuca Inlet region is mostly sedgeland heath, with large areas of wet scrub and small areas of wet

sclerophyll forest nearby (Brown and Podger 1982). The nearest rainforest is several kilometres away.

2.2.4 : Dating of the sediments.

Accurate dating of Early and Middle Quaternary western Tasmanian sediments is not possible at present. It is often difficult even to order different sediments in terms of age, and there may be confusion about the sequence of events within this time range. M. K. Macphail is developing a palynostratigraphy for Cainozoic western Tasmania, to supersede the classification of Stover and Partridge (1973, Partridge 1976) which is from the southern and eastern coast of Victoria.

The Linda Valley sediments are of Late Pliocene to earliest Pleistocene age. These sediments stratigraphically underlie the sediments associated with the Linda Glaciation which occurred at least 730,000 B.P. based on reversed palaeomagnetism. Extensive examination of sands and gravels underlying the microfossil bearing sediments has revealed no evidence of erratics. In an area which has undergone extensive Pleistocene glaciation this indicates a preglacial age (E. A. Colhoun pers. comm.), and thus earliest Pleistocene or older. Palynostratigraphy confirms that the Linda Valley sediments are at least this old on the basis of the presence of abundant *Nothofagus* subgenus *Brassospora* pollen, plus the presence of numerous other typically Tertiary forms (e.g. *Ascarina*, *Beauprea* and Araucariaceae) (M. K. Macphail pers. comm.). The presence of pollen of *Tubulifloridites pleistocenicus* and other taxa indicate that these sediments are unlikely to be older than Late Pliocene. Reworking from Tertiary sediments is unlikely to have occurred, since there are no Tertiary sediments anywhere upslope from the site.

The age of the Regatta Point sediments is determined mainly by palynostratigraphy. M. K. Macphail (pers. comm.) proposes an Early Pleistocene age for the Regatta Point sediments based on the presence of *Myrtaceidites verrucosus*, *Symplocopollenites austellus*, *Tubulifloridites pleistocenicus*, *Quintinia psilatispora*, *Stephanocolpites oblatus* and only trace levels of *Nothofagus* subgenus *Brassospora*. *Tubulifloridites pleistocenicus* and *S. oblatus* are only known from since the Late Pleistocene and *Nothofagus* subgenus *Brassospora* is common or abundant in all lowland post Eocene sediments as old as, or older than the Linda Valley sediments. Many common Tertiary forms (including many present in the Linda Valley sediments) are absent, so the sediments are

clearly Pleistocene. An age younger than Early Pleistocene is unlikely due to the presence of *M. verrucosus* and *S. austellus*. These taxa are unlikely to be reworked due to the relatively large quantities of *S. austellus* and the presence of a macrofossil in RPU1 of taxonomic affinity to *M. verrucosus*. Palynostratigraphy has previously been based on the well dated marine cores of the Gippsland and Bass Basins of Stover and Partridge (1973), but these are distant from Western Tasmania, and contain biases due to being of marine origin.

The fossil bearing clasts at Regatta Point occur in glacial outwash gravels containing Cambrian volcanic cobbles. The nearest source of Cambrian volcanics is over 20 km away. These cobbles, however, have weathering rinds considerably thicker than those associated with the Last Glaciation (E. A. Colhoun pers. comm.). The clasts contain an interglacial flora (see chapter 4) and must have been well lithified to survive the transport process, so must be at least as old as the interglacial before last. Arguments based on macrofossils that the RPU1&2 clasts are of similar ages and considerably older than the Regency Formation are presented in Chapter 6.

The Regency Formation overlies the Thureau Formation, which is derived from the Linda Glaciation (Fitzsimons *et al.* 1990). Hence, the Regency Formation is clearly younger than the Linda Valley sediments. Fitzsimons *et al.* consider that the Regency Formation conformably overlies the Thureau Formation and is from an interglacial that immediately followed the Linda Glaciation, and is therefore of Early Pleistocene age. The Thureau Formation contains highly weathered dolerite clasts, which are consistent with the Linda Glaciation, but the overlying Regency sediments contain very well preserved macrofossils, consistent with an almost total absence of weathering agents. E. A. Colhoun (pers. comm.), therefore, argues that this is unlikely to occur unless there was a considerable hiatus between the times of deposition of the Thureau and Regency Formations. The Regency Formation may, therefore, be from a more recent interglacial. It underlies sediments resulting from the Henty Glaciation, so must be Middle Pleistocene or older. The microfossil assemblage contains two extinct taxa, *Quintinia psilatispora* and *Gothanipollis perplexus*. *Quintinia* persisted in

Tasmania until the Late Pleistocene (Fitzsimons *et al.* 1990; E. A. Colhoun pers. comm.), and *G. perplexus* occurs near the base of the long core in Darwin Crater (M. K. Macphail pers. comm.). The Darwin Crater was formed by meteorite impact about 700,000 B.P., and the sediments at its base are believed to be of that age (E. A. Colhoun pers. comm.).

The Melaleuca Inlet sediments are likely to be the youngest of the sediments studied here. Palynology of the sediments indicates a Late Pleistocene age (M. K. Macphail pers. comm.) and wood from the Melaleuca Inlet sediments was radiocarbon dated at 38,800 ± 1,300 B.P. (SUA 5038). The radiocarbon age should be considered as a minimum age because the sediments are highly likely to have been contaminated by recent humic water (they occur in relatively unconsolidated gravels beneath sedgeland heath which is always associated with highly discoloured water, and the water table appears to be relatively mobile). ^{14}C concentrations in unpolluted samples decline logarithmically with age. 50,000 years is considered to be the limit of conventional dating. However, samples as young as 20,000 B.P. have low ^{14}C concentrations. Any contamination of such sediments with organic material of younger age will cause significant underestimates of age (Colhoun, 1986). The severity of this effect depends on the degree of contamination, but a reasonable working assumption is that any site with possible contamination and with a ^{14}C greater than 25,000 B.P. is outside the effective limits of radiocarbon dating.

The ages of the Linda Valley, Regatta Point, Regency and Melaleuca Inlet fossil deposits are, therefore, established palynologically, primarily by the presence of extinct taxa, or occasionally recently arrived ones, under the assumption of stepwise extinctions during the Pleistocene due to the glacial/interglacial cycle. A proportion of this work is concemed with the processes of extinction in western Tasmania. The use of palynostratigraphy alone for dating clearly may lead to some circularities. However, the independently dated long core records from off the coast of southern and eastern Victoria of Stover and Partridge (1973; Partridge 1986) largely corroborate the sequence of appearances and disappearances of the critical indicator taxa and do not conflict with any. Also, most of the extinct macrofossil taxa presented in this work would not have produced stratigraphically significant pollen types. The timing of extinctions is therefore treated conservatively.

The ages of the sites are therefore as follows. The Linda Valley

sediments are preglacial, and palynology indicates that they are Late Pliocene to Earliest Pleistocene. Palynology indicates that the Regatta Point clasts (RPU1&2) are Early Pleistocene but younger than Linda Valley. The Regency Formation is Early to Middle Pleistocene, younger than Linda Valley and palynology indicates that it is younger than RPU1&2. Palynology indicates that the Melaleuca Inlet sediments are likely to be Late Pleistocene and therefore younger than all the other sites. The Regatta Point clasts and the Melaleuca Inlet sediments were likely to have been laid down during interglacials or interstadials, the Regency Formation defines an interglacial, and the Linda Valley sediments are preglacial.

2.3 : Taphonomic Sites

2.3.1 : Hastings Pool : Rainforest Litter with Low Energy Transport

The pool referred to here as 'Hastings Pool' is a blocked sinkhole about 40 m x 12 m and about 0.75 m deep. It is located at 43° 22' S 146° 51' E (Fig 2.1) at an altitude of 390 m a.s.l. It occurs on Permian sediments underlain by Precambrian dolomites. The pool has no inflow or outflow stream. The pool appears to contain permanent water, but the presence of a dead *Nothofagus cunninghamii* stump in the deepest part of the pond indicates that it is relatively recent. The pool is surrounded by cool temperate rainforest co-dominated by *Eucryphia lucida*, *Atherosperma moschatum* and *Nothofagus cunninghamii* which is is unbroken for at least 100 m and has a relatively uniform canopy about 30 m high. The small size of the lake surrounded by tall dense forest results in very little wind disturbance. Neither forest nor pool show any sign of human interference. Leaves therefore enter the pool by dropping directly into the lake from overhanging trees or by being washed in during heavy rains along the forest floor. This lake therefore is a site where there is only very low energy and short distance transport of leaves before they enter the sediments.

Four litter samples from 0.25 m^2 areas of forest floor were cleared from near the pool from arbitrarily chosen sites around the lake. The canopies above the different samples were different. Sample 4 was from beneath a *E. lucida* tree, sample 5 was from beneath *Atherosperma*

moschatum and *N. cunninghamii* trees, sample 6 was from beneath a mixed canopy of *Anodopetalum biglandulosum, E. lucida* and *Atherosperma moschatum*, and sample 8 was taken from beneath a mixed canopy of *N. cunninghamii, E. lucida* with *Phyllocladus asplenifolius* nearby. Four samples were scooped from arbitrarily placed sites on the pool floor and washed with a sieve. Site 1 was from near the middle of the lake, and not under the canopy. Sample 2 was from towards the northern end under a *N. cunninghamii* tree. Sample 3 was from towards the western side under a closed canopy of *Anodopetalum biglandulosum, E. lucida* and *Atherosperma moschatum.* Sample 8 was from towards the eastern end of the lake, but not under the canopy.

2.3.2 : Old River and Melaleuca Creek : Riverine Scrub

Litter was collected from the Old River and from the bank of Melaleuca Creek (Figure 1 in Jordan *et al.* (1991) - Appendix 1) in order to obtain information about the taphonomy of species in the extant vegetation. The Old River site was on a beach near the river mouth. Vegetation upstream of, and around the deposit was dominated by wet scrub and sedgeland-heath, but included wet sclerophyll woodland and a small patch of diverse rainforest about 2 km upstream. The river is of moderate size and contains sections of normally high energy flow adjacent to the section of rainforest. The Melaleuca Creek site was below sections of high energy flow. Vegetation upstream of the site was almost entirely sedgeland-heath with some wet scrub along the creek bank.

2.3.3 : Lake Dobson : Lake in Diverse Subalpine Vegetation

Sediment samples collected, sorted and counted by Hill and Gibson (1986a) from Lake Dobson were used. Lake Dobson is a shallow lake about 200 m wide and about 400 m long, in south central Tasmania at about 1030 m above sea level. It is surrounded by diverse subalpine forest, woodland and sedgeland/heath. The forest and woodlands are dominated by *Eucalyptus coccifera, N. cunninghamii* or *Athrotaxis cupressoides.* The understoreys contain numerous shrub species particularly of the Epacridaceae, Asteraceae, Proteaceae and Myrtaceae. The Restionaceae,

Cyperaceae, Epacridaceae and Myrtaceae are prominent in the sedgeland/heath. Samples of lake sediments were taken along three parallel transects 10 m apart each made up of 52 samples. Two composite litter samples were also taken from the forest floor.

Glaciation	Age	Evidence	Fossil site	Age	Evidence
Margaret	max. at 17,000 ka[1]	Radiocarbon dates[1]			
			Melaleuca Inlet	Late Pleistocene (>38 ka)[2]	Radiocarbon, palynostratigraphy[2]
Henty	Middle Pleistocene[1]	underlies Margaret, overlies Moore Glaciation[1]			
Moore	Middle Pleistocene[1]	underlies Henty, overlies Linda Glaciation[1]			
			Landgon River	Middle Pleistocene[3]	∞ radiocarbon age, palynostratigraphy[3]
			Regency	Middle Pleistocene[1]	Weathering of erratics, overlies Linda glaciation, underlies Henty Glaciation [1]
			Regatta Point (RPU1 & 2)	Early Pleistocene[4]	Presence of pollen of extinct taxa and absence of prominent Tertiary taxa[4]
Linda#	Early Pleistocene[1]	Palaeomagnetism[1]			
			Linda Valley	Late Pliocene/ Early Pleistocene[5]	Palynostratigraphy, underlies till from Linda Glaciation[5]

Table 2.2. Summary of the ages of fossil deposits studied here, and of other relevant geological events in western Tasmania. The ages of the Langdon River and Regency sediments and the Henty Glaciation relative to each other are uncertain, as are the relative ages of the Linda Glaciation and the Regatta Point sediments. References [1] Fitzsimons and Colhoun 1991; [2] Jordan *et al.* 1991; [3] Colhoun *et al.* 1989; [4] M. K. Macphail pers. comm. [5] Macphail and Hill in press.

Chapter 3 : Fossil Taxonomy and Autecology of Related Taxa

3.1 : Introduction

Apart from a few taxa mainly from Tasmania (*Phyllocladus* by Hill (1989), *Nothofagus* by Hill (1991 b) and *Eucryphia* by (Hill 1991 a)) there has been very little taxonomic presentation of Australian Pleistocene macrofossils. Hill and Macphail (1985) illustrated and briefly discussed macrofossils of 16 taxa from the Early-Middle Pleistocene Regatta Point sediments, identifying nine of them as extant western Tasmanian taxa and not identifying seven of them. Colhoun and van der Geer (1987) illustrate one species, *Microstrobos niphophilus* and mention another coniferous twig from Late Pleistocene sediments from Rosebery Mine. Gibson *et al.* (1987) illustrate and discuss a single Late Pleistocene macrofossil species (*Donatia novae-zelandiae*) from the banks of the King River near Dante Rivulet. Fitzsimons *et al.* (1990) and Colhoun *et al.* (1989) record the presence of 14 and seven macrofossil taxa, respectively, without further justification. All of the macrofossils mentioned above are from western Tasmania.

The macrofossil taxa from the Regatta Point sediments, the Regency sediments and the Melaleuca Inlet sediments are illustrated here, and their identifications are justified. Where the same taxon occurs at more than one site it is only illustrated once, in most cases representing the oldest record. This comprehensive record and justification is useful since very few of these taxa have ever been illustrated as macrofossils, and their identification is usually based on characters, such as leaf cuticle and venation, which are not recorded anywhere else. Some of these taxa have been illustrated, and their identifications justified in Hill and Macphail (1985), Jordan and Hill (1991) and Jordan *et al.* (1991). They are included in this work for completeness and because the identifications of all the taxa recorded in Hill and Macphail (1985) and Fitzsimons *et al.* (1990) have been reappraised. Any previous records, illustrations and justifications are noted in the discussion for each taxon.

3.2 : Methods

Macrofossils were extracted from the sediments either by breaking the sediments open by hand, by gently macerating them in hot water containing about 5% hydrogen peroxide or by soaking the sediments in about 30% hydrofluoric acid (HF) for up to twenty-one days.* Specimens are stored in the Department of Plant Science at the University of Tasmania, either on rock or preserved in alcohol. To prepare cuticles, leaf fragments were placed in 10% aqueous chromium trioxide and kept warm until all other organic material had oxidized. For scanning electron microscopy, prepared pieces of cuticle or whole specimens cleaned in HF were placed on aluminium stubs and sputter coated with gold to a thickness of approximately 20 nm. Specimens were then studied using a Philips 505 scanning electron microscope operated at 15 kV. For light microscopy, prepared pieces of cuticle were neutralized with 5% ammonia, stained with 1% aqueous safranin O and mounted on slides in phenol glycerine jelly. Dispersed cuticle slides were prepared by gently macerating sediments in 5% hydrogen peroxide (for Melaleuca Inlet and Regency) or hydrofluoric acid until the sediments became disaggregated, then sieved through a 300 µm sieve, oxidized and stained as described above, then mounted on slides in phenol glycerine jelly. Fleshy material was removed from drupaceous seeds. Modern material was collected in the field, and taken from Hobart Herbarium (HO), CSIRO Herbarium Canberra (CANB) and Canberra Botanic Gardens Herbarium (C.B.G.)

3.2.1 : Nomenclature and Identification

There is uncertainty in the identification of every plant, living or dead, except of type specimens which have not been sunk into other species because they are correct by definition. This uncertainty is usually higher for fossil plants, since in general only fragments of the plant are available for identification, and these parts are often not the main organs used in identifying and describing modern plants. Most of the fossils studied here are leaves or leafy stems and most of the related modern taxa are primarily identified on the basis of floral characters. This uncertainty in identification is treated in different ways by different palaeobotanists, and therefore an explanation of the philosophy of identification used in this work is presented here.

This work adopts the philosophy of identification of fossil taxa

* Fractions greater than 500 µm were sorted completely, and subsamples of the residue greater than 300 µm were sorted for each sample processed.

presented by Collinson (1986). She asserts that fossils may be assigned to extant genera provided that thorough study shows that the fossils are consistent with the extant genus and inconsistent with any other extant genus. This philosophy is extended here to the species level since the fossils studied here are mostly very well preserved, with a wealth of morphological information and because many are likely to be very closely related to modern taxa due to their relatively young age.

Many characters which are largely ignored in the taxonomy of living plants can be used in identifying fossil leaves. These include cuticle and venation characters. Wells and Hill (1989 b) have shown that cuticle characters are highly diagnostic among the imbricate-leaved Podocarpaceae. Cuticle characters of *Banksia* series *Salicinae* are extremely consistent within species, with little difference between leaves on single plants, slight differences between plants within populations, slightly larger differences between populations of species, and major disjunctions between species (G. J. Jordan unpublished). R. J. Carpenter (pers. comm.) is currently undertaking an extensive study of the taxonomic significance of cuticle characters within the Proteaceae, and these appear to be highly diagnostic, particularly to generic and subgeneric levels.

There are two general related aims of this project : one is to identify taxa which have become extinct from Tasmania during the Pleistocene, and the other is to identify changes in vegetation during this time that may be have been associated with these extinctions, or may help explain them. The nature of these aims affect the nature of the identifications made in this work, although they sometimes have conflicting effects. To identify extinct species, clear and significant differences between the fossil and any extant species need to be established. Hence, a fossil is not described as being extinct in this work unless it is clearly distinct from any extant taxon. Many extinct taxa may be included in extant taxa simply because insufficient taxonomic information has been found to distinguish them (e.g. where the species is extinct, but the genus is extant and the fossils are assigned to the genus, or sometimes when a species is described as 'aff.' or 'cf.' an extant species). Where a fossil species can be clearly assigned to a higher order taxon of relatively small size this becomes a task of eliminating all extant

species, e.g. in the case of *Banksia strahanensis*, the fossil is clearly a member of *Banksia* section *Oncostylis* (Jordan and Hill 1991) and it is only necessary to eliminate the other 22 species of this section. On the other hand, if the fossil does not clearly belong to a small higher order taxon the task becomes more difficult e.g. *Rubus* has at least 250 species worldwide, which are morphologically variable, with unclear species delimitation. More difficult still are taxa where even family assignations are uncertain, e.g. the taxon described as '? Proteaceous genus unknown #2'. In these cases it is only possible to establish regional extinction, even though it is likely that they are globally extinct, at least at the species level. Establishing regional extinction of vascular plants is relatively easy, since the flora of Tasmania is well known with only about 1500 native vascular plant species (Buchanan *et al* 1989).

Identifications for vegetation reconstructions have different requirements than those trying to identify extinctions. Here identification of a fossil as an extant species requires a considerable amount of taxonomic information. If a fossil shares many characters with an extant species, and is consistent with it, and is distinct from all other extant species, it should be assigned to the extant species, otherwise it should be identified to genus or family level, perhaps with reference to an extant species (e.g. by using 'cf.').

Conventions are used to signify the strengths of the identifications of fossils. The use of an extant plant name (whether at family, genus or species level) without qualification indicates that there is a very high probability that the fossil belongs to that taxon. The use of 'aff.' before a taxon name indicates that the fossil is from a taxon which is closely related to the extant taxon. The use of 'cf.' indicates that the fossil bears similarities to the extant taxon, there is a considerable amount of taxonomic information, but the fossil differs from the extant taxon in some way. The use of '?' before a name implies that the fossil is consistent with the extant taxon, but there is insufficient taxonomic information to make a strong determination.

Distributions and taxonomy follow Allen (1961), Curtis (1963; 1967), Curtis and Morris (1975), Scott *et al.* (1976), Stanley and Ross (1983, 1986, 1988), New (1984), Duncan and Isaac (1986), Brock (1988), Buchanan *et*

al. (1989), de Laubenfels (1989), Wilson and Johnson (1989), Hnatiuk (1990), Harden (1990; 1991) and Dalton *et al.* (1991). Authorities for all species are included in Appendix 1.

3.3 : Macrofossil Taxonomy

3.3.1 : Musci

Southern Australian mosses can often be identified using only gametophyte material based on leaf shape, phyllotaxy and particularly cell shape and distribution in leaves. These characters are readily apparent in well preserved fossil material, such as that described here. Family relationships within the mosses are not clearly understood, due to great morphological variation within species, and considerable convergence. Mosses are generally undercollected, so the bryoflora of Tasmania is only moderately well known. Discoveries of new species, and particularly new records are relatively common. Mosses are generally quite fragile and have no cuticle and appear to be poor candidates for fossilization, particularly in cases of high energy transport, and macrofossils have rarely been recognised in Cainozoic sediments in Australia. Moss spores are reasonably common in Cainozoic sediments, but their taxonomy is not sufficiently well known to assign affinities to many of them, also many palynologists are unfamiliar with moss spores. There are, however, many records of macrofossils of mosses from peats in the northern Hemisphere, mainly of Late Quaternary age but also of Tertiary, Early and Middle Pleistocene ages (Dickson 1973).

Many moss species have very broad distributions (e.g. many Tasmanian species occur widely in both hemispheres, including *Hypnum cupressiforme*, *Grimmia trichophylla*, *Polytrichum juniperinum* and *Bryum argenteum*, more occur in Australia, New Zealand and South America, including *Polytrichadelphus magellanicus*, *Ptychomnion aciculare* and *Thuidium furfurosum* and many more are common to Australia and New Zealand (Scott *et al.* 1976)). There is some endemism of species, but very little of genera. This may be partly due to the astonishing powers of vegetative regeneration of many mosses allowing for widespread dispersal.

aff. *Barbella nitens* (RPU2)

Specimens examined : RPU 592-595

Discussion : These distinctive fossils (Figures 3.1 a, b & e) are entirely consistent with *Barbella*. The leaves are arranged in 5 ranks, but are not flattened. This occurs weakly in *Barbella nitens* (Figure 3.1 c), the only species of this genus in southern Australia and clearly in the closely related *Papillaria crocea* (Figure 3.1 g) but occurs elsewhere among mosses of southern Australia only in *Leucobryum* species which (unlike the fossils) have distinctive hyaline lamina cells, and *Conostomum* species which (unlike the fossils) have prominent nerves and single papillae on each cell (Scott *et al.* 1976). The fossils have similar leaf shapes to *B. nitens* (Figure 3.1 d) with wide bases tapering quickly to elongate points, with the sides of the leaf bases wrapped around, but not fused to the stems. The lamina cells (Figure 3.1 e) are porose, elongate (2-4 : 1) and rhomboidal in the main part of the lamina, but irregularly shaped towards the base. Papillae are apparent on the leaf margins. All other known species of *Papillaria* from southern Australia differ from the fossils in having densely papillose leaf lamina cells of uneven sizes across the lamina and narrower leaf bases. The fossils differ from *B. nitens* in cell shape and wall thickness and porosity, and having leaves clearly in five ranks. The only specimen of *B. nitens* that I have seen (Figure 3.1 f) also has much thicker walled cells than the fossil, which are somewhat sinuous and scarcely porose and leaves which taper more rapidly than those of the fossil. *B. nitens* is, however, a rare and probably undercollected species (Scott *et al.* 1976) and the fossils may fall into the extant range. The fossils, therefore, are clearly of the genera *Papillaria* or *Barbella* and are probably an extinct species. *Papillaria* and *Barbella* are members of the Meteoriaceae which are pendulous epiphytes mostly of tropical rainforest. *B. nitens* is an epiphyte of wet forests from eastern Australia and New Zealand.

***Ptychomnion aciculare* (RPU2)**

Specimens examined : RPU 580-584

Discussion : These fossils are indistinguishable from the distinctive extant species *Ptychomnion aciculare*. The fossils have broadly ovate;

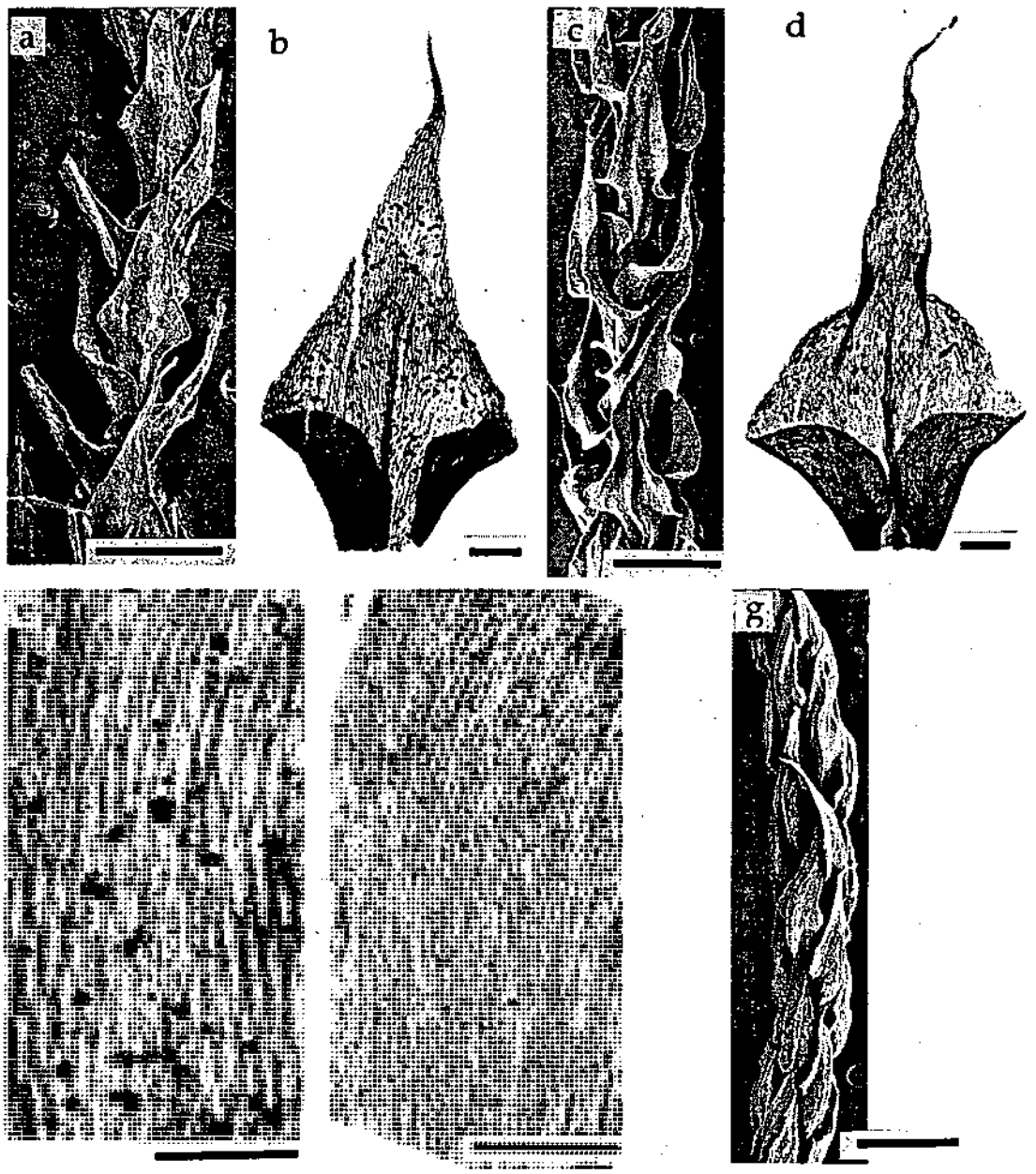


Figure 3.1 : Meteoriaceae (Musci). a, b & e : Fossil aff. *Barbella nitens* from RPU2. c, d & f : Extant *B. nitens*. g : Extant *P. crocea*. a, c & g : Stems. Note that the fossil and *Papillaria crocea* have leaves in five ranks. b & d : Leaves. Note the sheathing leaf bases, and nerve failing in midleaf. e & f : Lamina cells from off centre midleaf. Scale bars for a, c & g = 0.5 mm, for b & d = 100 µm, for e & f = 50 µm.

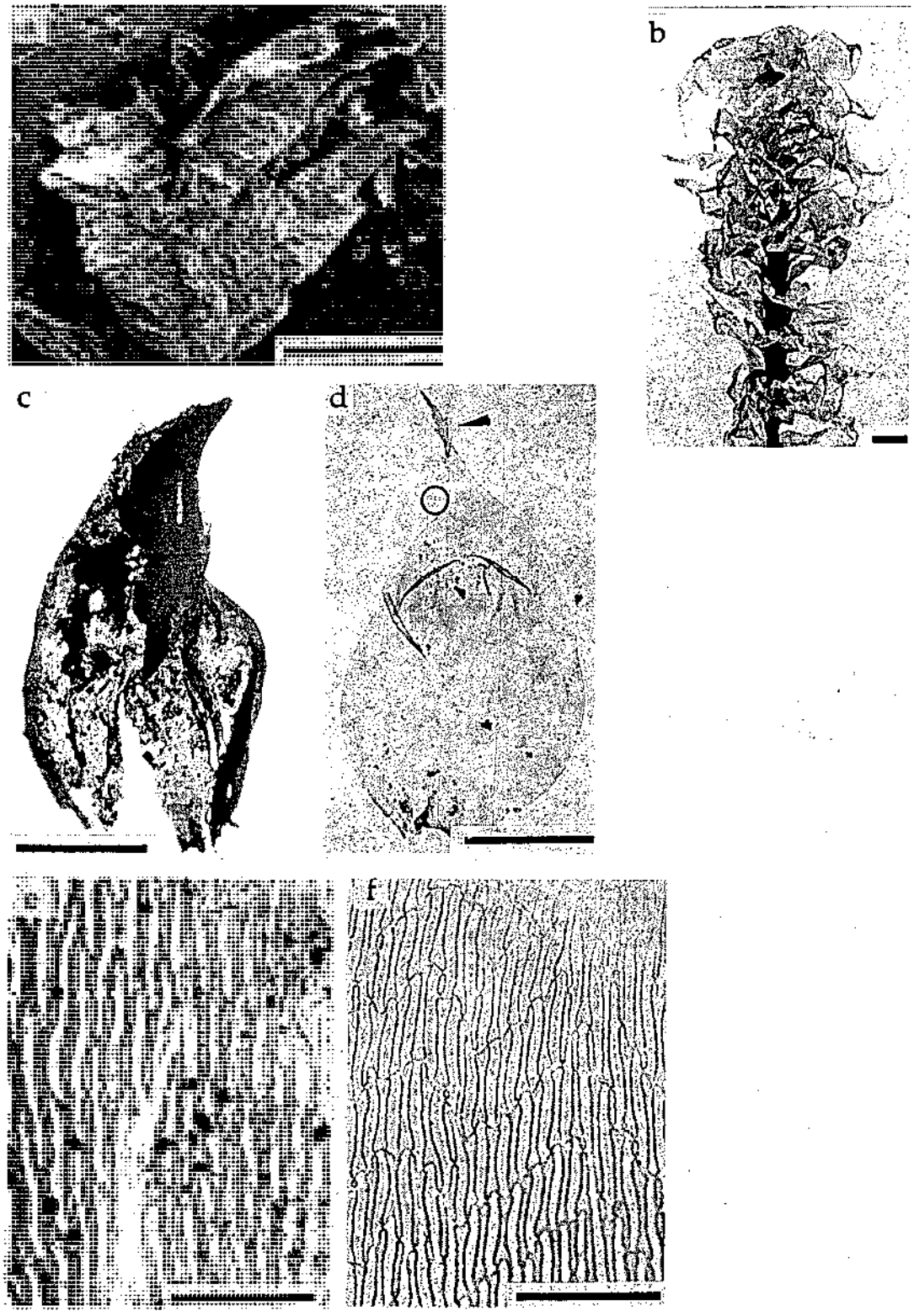


Figure 3.2 : *Ptychomnion aciculare* (Musci : Ptychomniaceae). a, c & e : Fossil material from Regatta Point. b, d & f : Extant material. a & c : Stem fragments. Note the toothed leaf apex on the fossil (arrow). b & d : Leaves. Note the similar leaf shape, the lack of nerve and the toothed leaf apex on the extant specimen (arrow). e & f : Lamina cells from off centre midleaf. Note the porose cell walls and similar cell shape. Scale bars for a, b, c & d = 1 mm, for e & f = 50 µm.

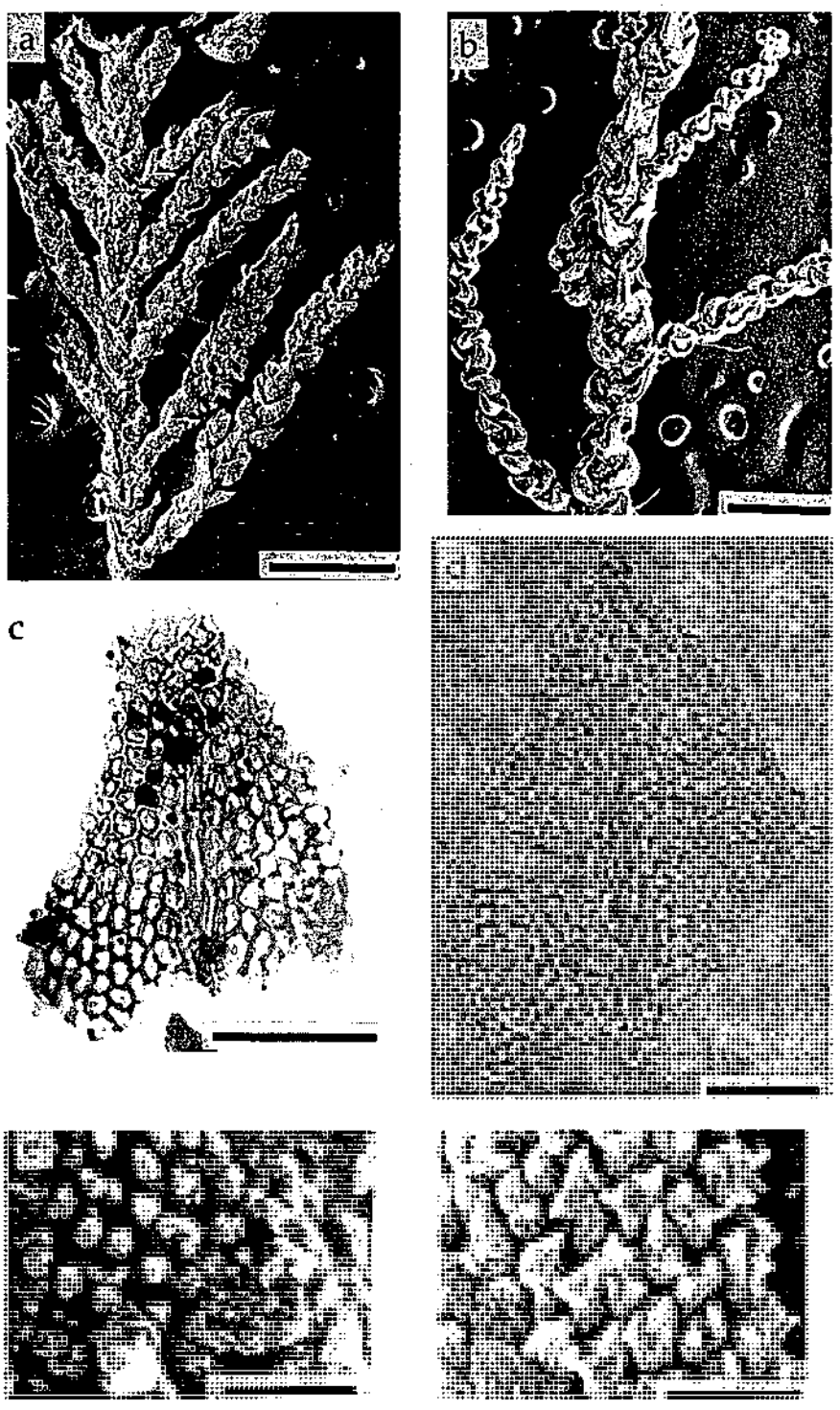


Figure 3.3 : *Thuidium* (Musci : Thuidiaceae). a, c & e : Fossil *Thuidium* aff. *furfurosum* from Regatta Point. b, d & f : Extant *T. furfurosum*. a & b : Leafy stems. c & d : Leaves. Note the nerve failing below the apex. e & f : Detail of leaf showing papillae. Scale bars for a & b = 0.5 mm, for c & d = 50 µm, for e & f = 10 µm.

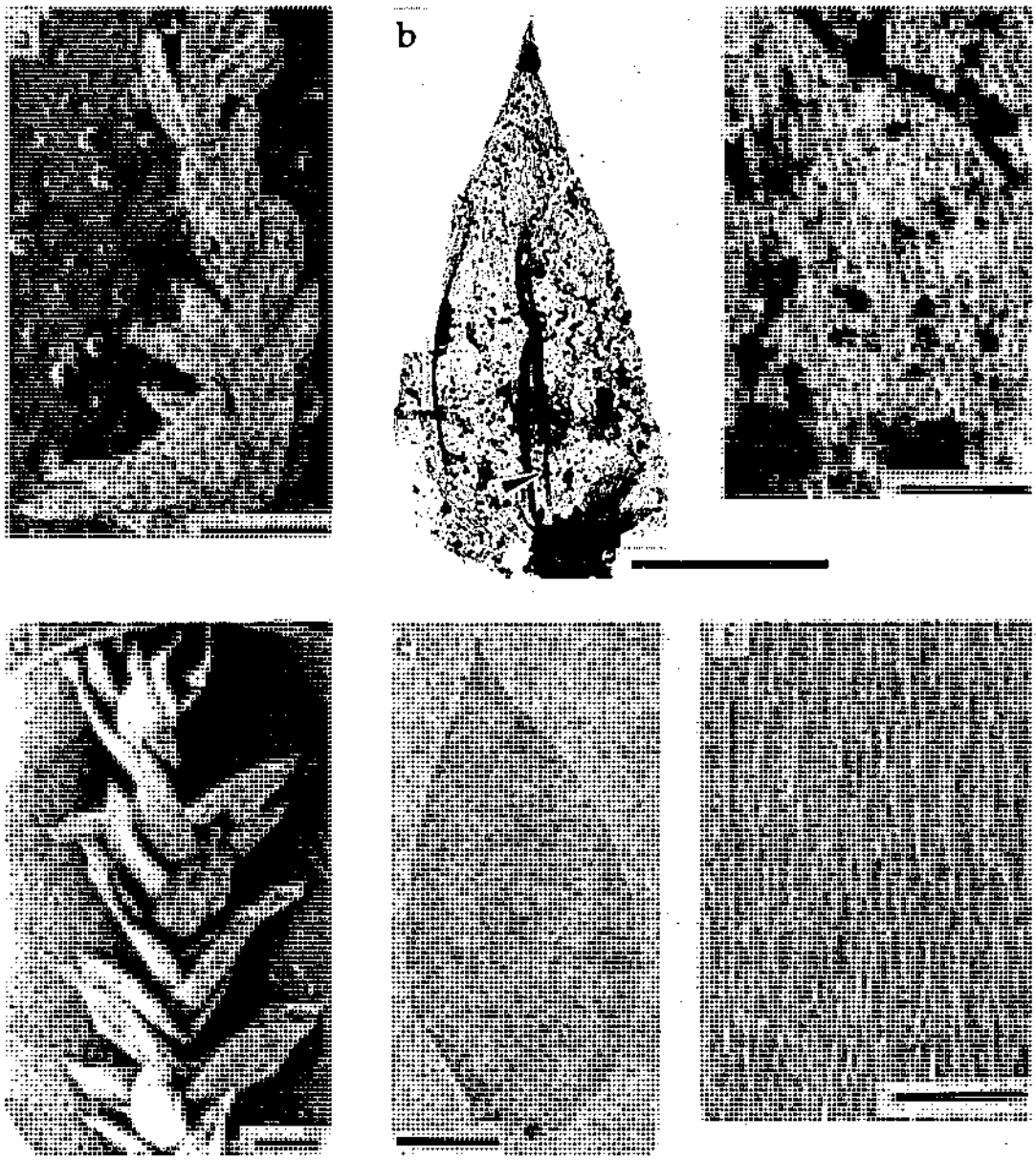


Figure 3.4 : *Trachyloma* (Musci : Pterobryaceae). a, b & c : Fossil cf. *Trachyloma* from Regatta Point. d, e & f : Extant *T. planifolium*. a & d : Leafy stems. Note the similarity in habit. b & e : Leaves. Note the similarity in leaf shape, the smaller size of the fossil, and the weak nerve present in the fossil (arrow) but absent in the extant specimen. c & f : Lamina cells from off centre midleaf. Note the similarity in shape. Scale bars for a & d = 1 mm, for b & e = 0.5 mm, for c & f = 50 μm.

identification. *Trachyloma planifolium* is a rainforest epiphyte of eastern Australia and New Zealand. Scott *et al.* (1976) the other species recorded for Tasmania, *T. diversinerve*, to be conspecific with *T. planifolium.*

***Weymouthia mollis* (RPU2)**

Specimens examined : RPU 4592

Discussion : This fossil (Figures 3.5 a, c, d & g) is indistinguishable from the distinctive extant species *Weymouthia mollis* (Figures 3.5 b, e, f & h). The strongly channelled ovate leaves with obtuse apices; elongate, sinuous midleaf cells; abruptly contracted leaf base with conspicuous alar group of thick walled isodiametric cells and short apical cells are sufficient to identify this taxon. Superficially similar species include *W. cochlearifolia* and *Lembophyllum divulsum*, which differ in having almost circular leaves; *Camptochaete* species, which have distinctly shorter cells and *Papillaria* species, which have acute leaf apices and papillose cells.

Weymouthia mollis is a common pendulous epiphyte in wet forest in Tasmania, Victoria, New Zealand, Lord Howe Island and South America.

Other Mosses (RPU2)

Specimens examined : RPU 596-598 (moss species 1)
RPU 599-602 (moss species 2)

Discussion : Other distinctive moss fossils occur in the Regatta Point sediments. Two taxa from RPU2 are illustrated in Figures 3.6 c - g. These have not been attributed to any extant taxon.

3.3.2 : Pteridophyta

Pteridophytes generally have fragile cuticle, but often have robust foliage, so that the identification of fossil pteridophytes usually depends on gross morphology. Identification of fossil pteridophytes without the presence of sori is, therefore, often tentative.

Page (1979) presents evidence that ferns have spores that are capable of transport by wind and seem generally to have moderately long term viability (typically of the order of a few years). Many species, however occur in relatively wind free forest understoreys so their spores are unlikely to be

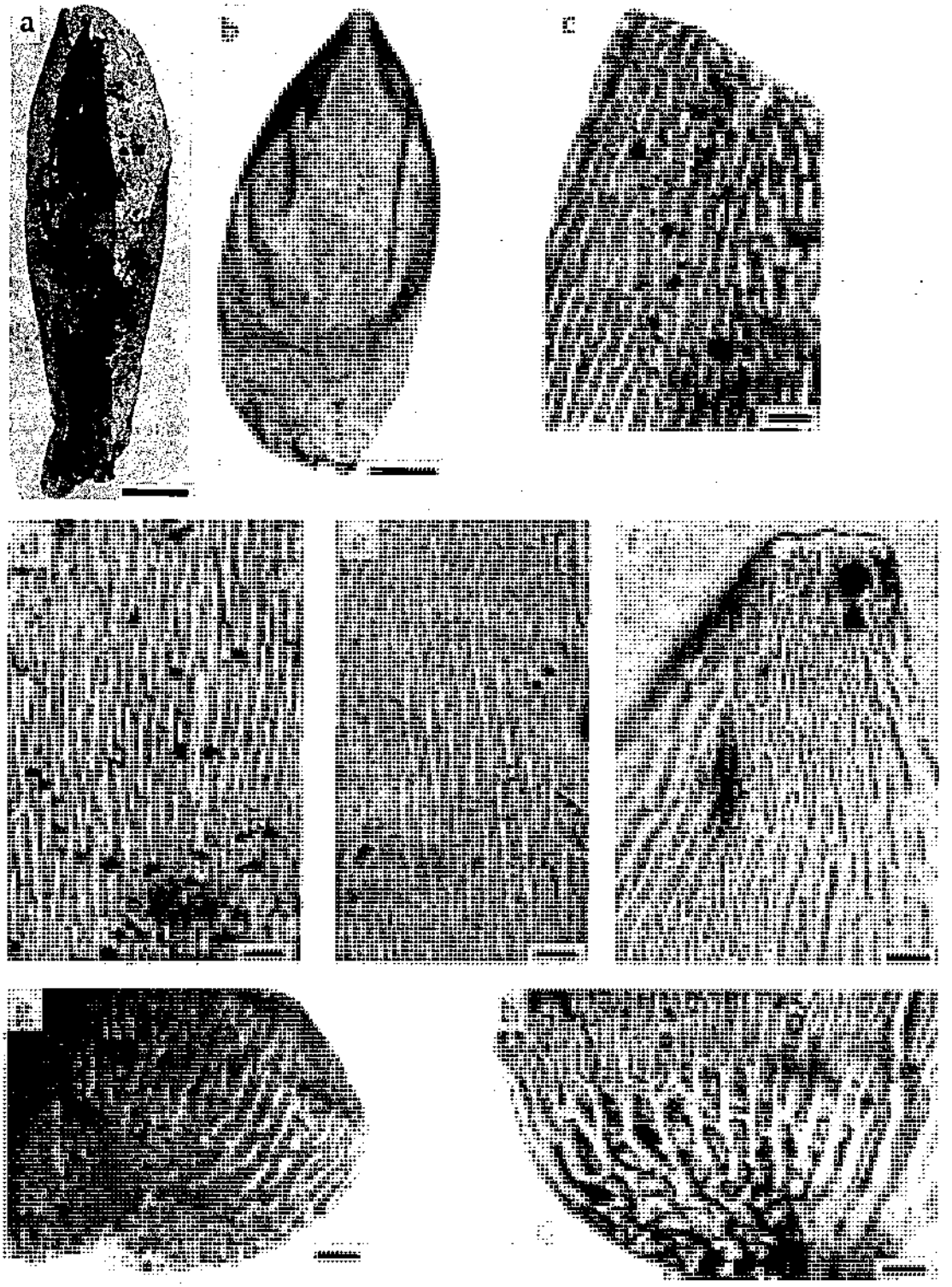


Figure 3.5 : *Weymouthia mollis* (Musci : Meteoriaceae). a, c, d & g : Fossil *W. mollis* from Regatta Point. b, e, f & h : Extant *W. mollis*. a & b : Leaves. Note that the fossil leaf is folded over on itself all along the left side and in the basal half of the right side, and the extant leaf is folded in at the apex on both sides, and is missing the base on one side. c & f : Cells from leaf apex. d & e : cells from off centre midleaf. g & h : Cells from leaf base at side (alar cells). Note the short, thick walled cells. Scale bars for a & b = 0.2 mm, for b - h = 50 µm.

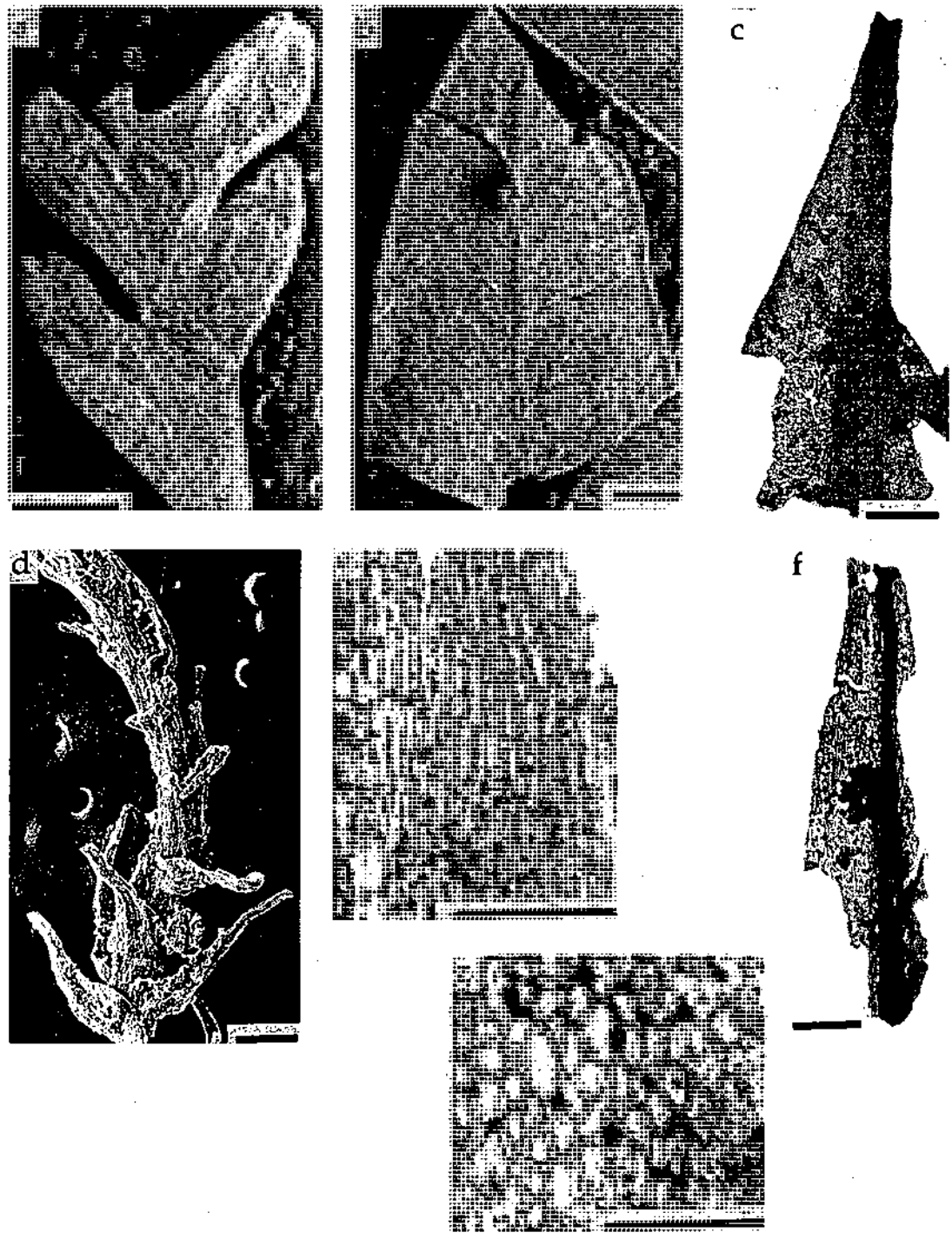


Figure 3.6 : Unidentified mosses and probable ferns : a & b : Probable fern frond fragments of uncertain affinities. c, d & g : Unidentified moss species 1. c : Leaf. Note the strong nerve. d : Stem. g : Lamina cells from off centre midleaf. Note the nearly isodiametric thick walled cells. e & f : Unidentified moss species 2. e : Lamina cells from off centre midleaf. Note the elongate cells. The stems of this fossil taxon appear similar to species 2. f : Leaf. Note the strong midrib. Scale bars for a & b = 1 mm, for c, d & f = 0.2 mm, for e & g = 100 μm.

dispersed by wind. Water may play apart in dispersal of some ferns. Many ferns are early successional plants, and therefore need to be relatively well dispersed. There is considerable evidence of establishment of such ferns and also of some less ruderal species after major disturbance (e.g. volcanic eruption) which is undoubtedly the result of spore dispersal (Page 1979). It is not known, however, how many non-ruderal ferns normally regenerate from spores, since many species apparently depend on vegetative means for reproduction, and many have specialised vegetative propagules (e.g. *Asplenium bulbiferum* produces small deciduous bulbils on its leaves).

Dicksoniaceae

***Dicksonia antarctica* (RPU1&2)**

Specimens examined : RPU 417, 454, 469, 603-640, 1943-2420.

Discussion : Both fertile (Figure 3.7 a) and infertile fragments of fronds which are consistent with *D. antarctica* occur in the Regatta Point sediments. The morphology of fertile fragments with margin recurved to partly cover the sorus, and semicircular intramarginal indusium partly covering the remainder of the sorus is diagnostic of the genus (Fig 3.7 b) and this is apparent on the fossils. This represents the earliest macrofossil record of this species, although the spores *Matonisporites ornamentalis*, which are attributed to *Dicksonia* are known from south-eastern Australia sediments at least as far back as the Eocene (Stover and Partridge 1973).

Dicksonia antarctica is a tree fern which occurs widely in wet forests of south eastern Australia, including Tasmania. Although *Cyathea* spores are common in the Regatta Point and Regency sediments, and present in the Melaleuca Inlet sediments, no macrofossils in these sediments can be reliably attributed to *Cyathea*. It is possible, however, that some of the infertile frond fragments attributed to *D. antarctica* could be *Cyathea*. The proportion of fertile to infertile fossil frond fragments is consistent with the proportion found in modern *D. antarctica* litter, so it is unlikely that a high proportion of the fossil infertile frond fragments are *Cyathea*.

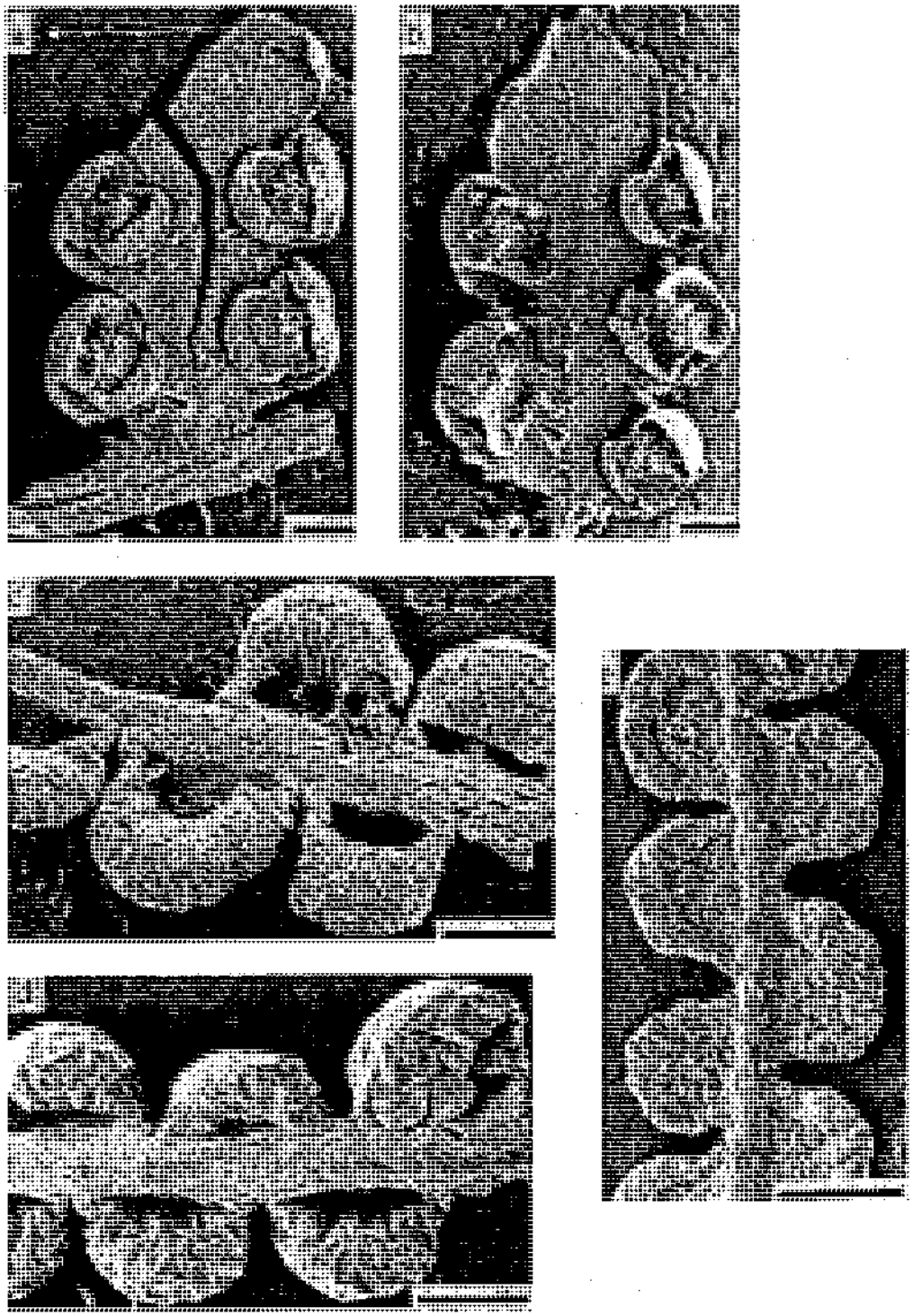


Figure 3.7 : Ferns. a & b : *Dicksonia antarctica* (Dicksoniaceae) frond fragments. Note the sori (arrows). a : Fossil fragment from Regatta Point. b : Extant frond fragment. c, d & e : *Gleichenia* frond fragments. Note the twin sori in c & d (arrows). c : Fossil *G. dicarpa* from Melaleuca Inlet. d : Extant *G. dicarpa*. e : Fossil from Regatta Point. Scale bars for a & b = 1 mm, for c, d & e = 0.5 mm.

Gleicheniaceae

***Gleichenia dicarpa* (ME)**

Specimens examined : ME 35-80.

Discussion : This fossil taxon was illustrated by Jordan *et al.* (1991). These frond fragments (Figure 3.7 c) are typical of *Gleichenia* and some fragments show the two sori enclosed in a pouch-like false indusium characteristic of *G. dicarpa*. *Gleichenia dicarpa* (Figure 3.7 d) is now widespread and common in sedgeland-heath and wet scrub communities from lowland to intermediate altitudes in Tasmania and elsewhere.

***Gleichenia* sp. (RPU1)**

Specimens examined : RPU 641

Discussion : These fossil frond fragments (Figure 3.7 e) are indistinguishable from extant *Gleichenia* and have the characteristic 'pouches' of this genus. These fragments do not have sori, and are consistent with several extant species of *Gleichenia*. *Gleichenia* species are widespread in wet, poorly drained, well lit areas of Australia and elsewhere. They occur in a wide range of climates.

Other Ferns (RPU2)

Specimens examined : RPU 642-644 (Fern taxon 1)
RPU 681-685 (Fern taxon 2)

Discussion : Infertile frond fragments of other, unidentified, fern taxa from the Regatta Point sediments are illustrated in Figures 3.6 a & b.

3.3.3 : Coniferae

Cupressaceae

***Callitris* /*Actinostrobus* species(RPU2)**

Specimens examined : RPU 520,645-680, 1423-1446

Description : Stems with tricussate imbricate leaves. Leaves thick, decurrent. Adnate base of leaf about 1.5 mm long, about 0.6 mm broad, triangular, with scarcely expanded keel in transverse section. Free portion of leaf appressed, rhomboidal about 0.9 mm long, about 0.6 mm broad, short marginal frill present. Stomata with prominent, often split, raised rings

of cuticle surrounding the aperture, evenly distributed on lateral faces of abaxial leaf surface, occasional on adaxial and abaxial surfaces of free part of leaf, subsidiary cells not distinguishable from epidermal cells. Epidermal cells of adnate part of leaf more or less rectangular, about 2-3 times longer than broad, cells of free part of leaf rhomboidal, porose walled.

Discussion : These fossils (Figure 3.8 a) have tricussate phyllotaxy (i.e. leaves attached in equal whorls of three in which each whorl is rotated around the stem at an angle of 60° to the previous whorl, hence being the equivalent of opposite and decussate phyllotaxy except with three leaves at each node rather than two). Within the conifers tricussate phyllotaxy occurs only in the closely related genera *Callitris* and *Actinostrobus* apart from aberrant forms of other taxa. The cuticular morphology of stomates and epidermal cells of the fossils (Figures 3.8 e & g) are consistent with these genera (e.g. Figure 3.8 f & h). Hence, these fossils almost certainly were derived from *Callitris*, *Actinostrobus* or a very closely related extinct genus. The cross sectional shape of the decurrent leaf bases is diagnostic of groups of species of *Actinostrobus* and *Callitris* (Offler 1984). The two species extant in Tasmania, *C. rhomboidea* (Figure 3.8 b) and *C. oblonga*, are among the species which have leaves with prominent expanded keels which form a bulbous ridge along the length of each leaf. Other species (*C. macleayana*, *C. baileyi*, *C. drummondii*, *C. roei*, *A. arenarius* and *A. pyramidalis*) may have the keels scarcely expanded (Offler 1984) as in the fossil. The final group have leaves which are not keeled and are convex in cross section (Figure 3.8 c). The keeled species all have stomata distributed on the concave surfaces of the leaves. The unkeeled species have stomata restricted to the grooves between leaves. *Actinostrobus* species normally have the free part of the leaf more or less spreading but occasional forms have the leaves more or less appressed (Figure 3.8 d). It is, therefore, not possible to determine at this stage to which genus these fossils belong, but the species is clearly extinct from Tasmania.

Species of *Callitris* and *Actinostrobus* now mainly occur in dry areas of Australia (Figure 3.9). There are, however, a few species of *Callitris* which occur in wet areas, but in warmer climates than now occur in Tasmania. *Callitris macleayanus* occurs on rainforest margins of Northern New South

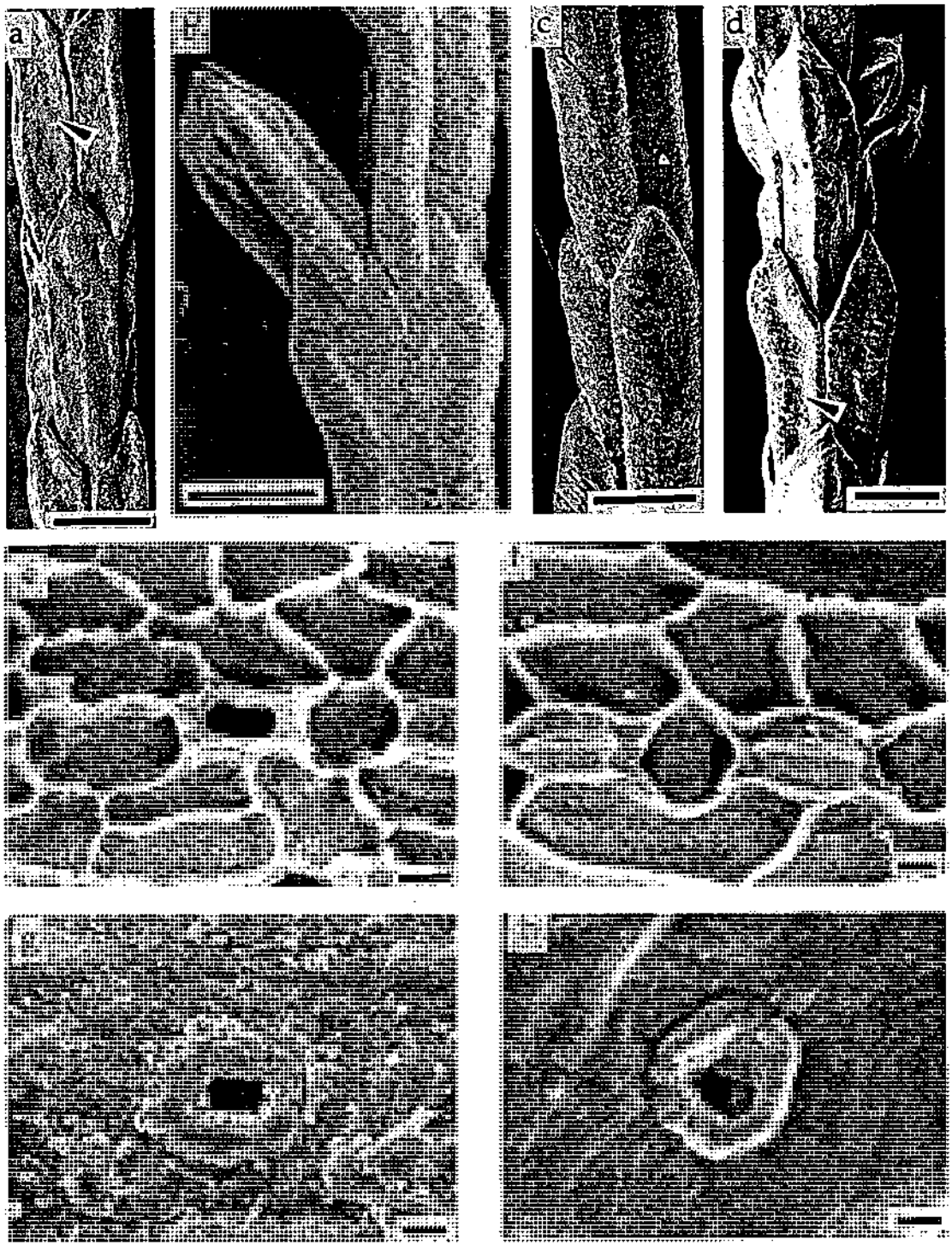


Figure 3.8 : *Callitris* and *Actinostrobus*. a - d : Stems. Note the stomata (arrows) and the varying development of keels on the leaves. a : Fossil *Callitris/Actinostrobus* from Regatta Point. b: *C. rhomboidea*. c : Extant *C. columellaris*. The stomata are hidden in the grooves between the leaves. d : *A. pyramidalis*. Note the slightly spreading free (apical) part of the leaf (less spreading than normal in *Actinostrobus*). e - h : Cuticles. e & g : *Callitris/Actinostrobus* from Regatta Point. f & h : Extant *C. rhomboidea*. e & f : Inner surfaces showing stomata. The flanges of cuticle covering the aperture (apparent in the extant specimen) may have eroded from the fossil. g & h : Outer surfaces. Note the prominent raised ring of cuticle surrounding the stomatal aperture (Florin ring). Scale bars for a, b, c & d = 0.5 mm, for e, f, g & h = 10 µm.

Wales. *Callitris* species from New Caledonia occur as riparian plants in relatively wet areas. *Callitris intratropica* is widespread in the wet/dry tropics of Northern Australia. Its distribution appears to be limited by high fire frequencies. *Callitris* and *Actinostrobus* species have dry, winged seeds which are relatively massive, and are unlikely to be well dispersed.

Figure 3.9 : Extant distribution of *Callitris* and *Actinostrobus*.

Podocarpaceae

aff. *Dacrydium/Dacrycarpus* (RPU2)

Specimens examined : RPU 525,532,542&559

Description : Stems with loosely imbricate, spirally arranged leaves. Leaves lanceolate, apex acute, margins ciliate, stomata common on adaxial surface. Cuticle of adaxial surface with buttressing of anticlinal walls of epidermal cells, stomata in two equal longitudinal bands, each band composed of 6-8 uniseriate rows of stomata oriented parallel to long axis of leaf. Stomata elongate, with raised rings of cutin surrounding the apertures, guard cells with large cuticular flanges, lateral guard cells occasionally

shared between stomata. Epidermal cells of abaxial surface elongate, rectangular, without buttressing.

Discussion : The identification of these fossils (Figure 3.10) is based on only four relatively poorly preserved leafy stems. The fossils are consistent in all characters with Podocarpaceae and have characteristic podocarpaceous stomata (compare with Figure 3.13 d). Imbricate leaved species of other conifer families with spiral phyllotaxy differ in group defining cuticular characters, e.g. *Athrotaxis* species have imbricate foliage (Figures 3.17 a, b & c) but have distinctive cuticle (Figure 3.17 d).

The fossils have characteristics considered diagnostic of both *Dacrycarpus* (Figure 3.11 a & b) and of *Dacrydium* (Figure 3.11 c & d) by Wells and Hill (1989 b). They are inconsistent with all other genera of Podocarpaceae. Cell wall buttressing is typical of *Dacrydium*, but all extant species have prominent buttressing of the abaxial surface, whereas *Dacrycarpus* species have smooth cell walls, like the abaxial surface of the fossil. The well developed cutin flanges on the guard cells are more typical of *Dacrycarpus* than *Dacrydium*. The acute leaf apices apparent on one fossil specimen are unlike any extant *Dacrydium*, which all have obtuse leaf apices. The fossil has trichomes along the leaf margins, which are not known in any fossil or extant *Dacrycarpus* and *Dacrydium* species, but these may be the result of reduction of a marginal frill. Marginal frills are known in two extant scale leaved species of *Dacrydium*, extant *Dacrycarpus dacrydioides* and at least two fossil species, *Dacrycarpus eocenica* from the Eocene Anglesea sediments of southern Victoria (Hill and Carpenter 1991) and *Dacrycarpus praecupressinus* from the Tertiary coals at Yallourn (Cookson and Pike 1953). The large number of rows of stomata (6-8) per band on each side of the leaf are usual in *Dacrydium* but are not known in *Dacrycarpus*, except in *Dacrycarpus dacrydioides*. It is therefore not possible to allocate them at this stage to either *Dacrydium* or *Dacrycarpus*. They do share several characters with the extant New Zealand species *Dacrycarpus dacrydioides* : acute, lanceolate, slightly spreading leaves with marginal frills, unbuttressed anticlinal walls of the epidermal cells of the abaxial surface, about six longitudinal rows of stomata per band on each side of the adaxial leaf surface. There are also significant differences

between the fossils and *Dacrycarpus dacrydioides* : the marginal frills of the fossil are developed into cilia and extend the length of the leaf, and the anticlinal walls of the epidermal cells of the adaxial surface are buttressed. The fossil taxon is therefore an extinct species from a genus which is extinct in Australia and possibly globally. It is not described here as a new species only because its generic affinities are unclear.

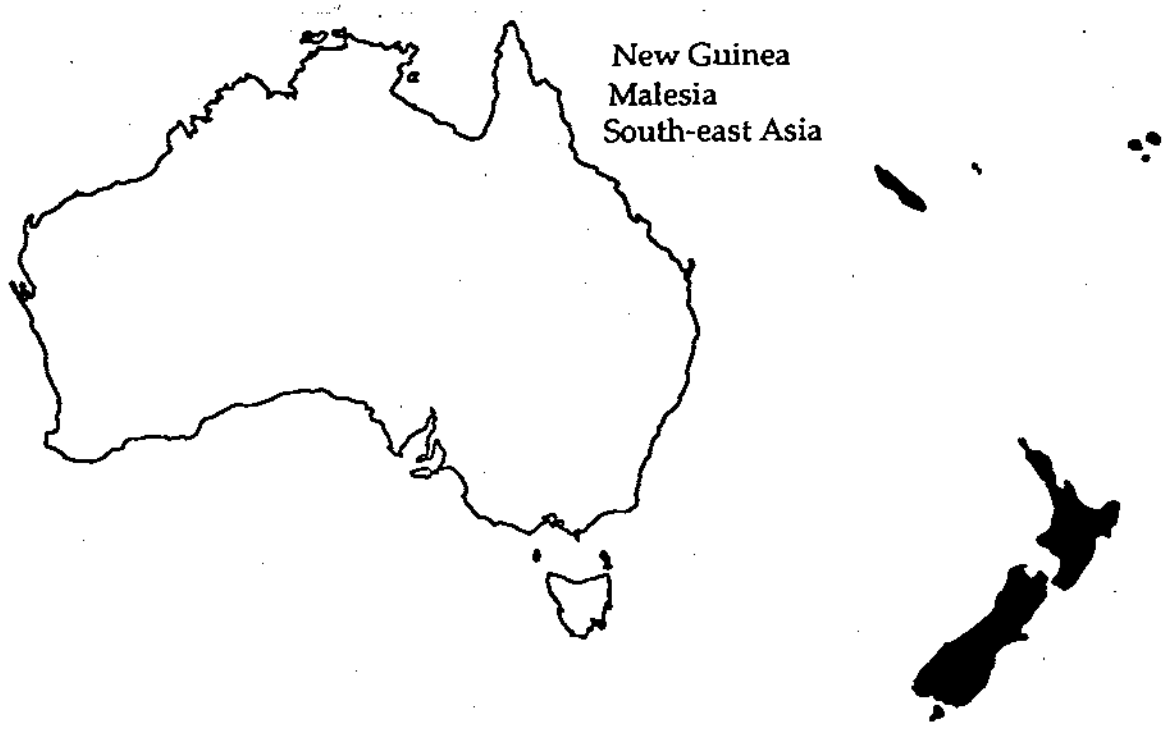


Figure 3.12 : Extant distribution of *Dacrycarpus* and *Dacrydium*.

Living *Dacrydium* and *Dacrycarpus* have similar distributions (Figure 3.12), which include New Zealand, South Pacific and Malesia. They are extinct from Australia, but have extensive Tertiary fossil records from south-eastern Australia, particularly Tasmania (Wells and Hill 1989 a; Hill and Carpenter 1991). *Dacrycarpus dacrydioides* occurs widely in rainforest in New Zealand. These taxa have seeds enclosed in fleshy arils, and may be bird dispersed.

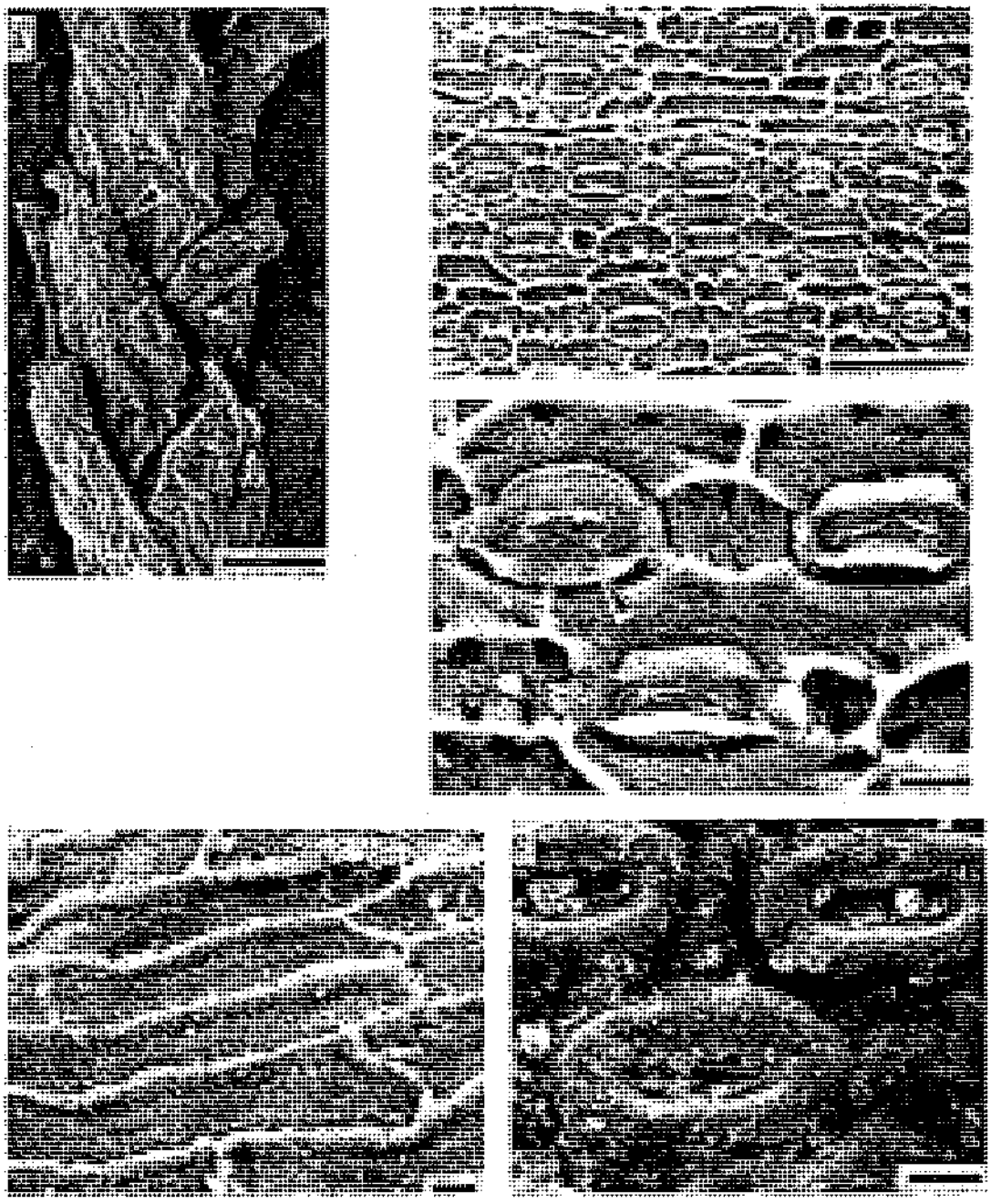


Figure 3.10 : Fossil aff. *Dacrycarpus/Dacrydium* from Regatta Point. a : Leafy stem. Note the marginal trichomes (arrowed). b : Inner surface of cuticle of adaxial leaf surface. Note the stomata arranged in lines and the buttressed anticlinal cell walls. c : Inner surface of cuticle of adaxial surface of leaf. Note the prominent cutin flange (arrow). d : Inner surface of cuticle of abaxial leaf surface. Note the absence of buttressing of any walls. e : Outer surface of cuticle of adaxial surface of leaf. Note the prominent florin rings (rings of raised cuticle around the stomatal aperture). Scale bars for a = 0.5 mm, for b = 50 µm, for c, d & e = 10 µm.

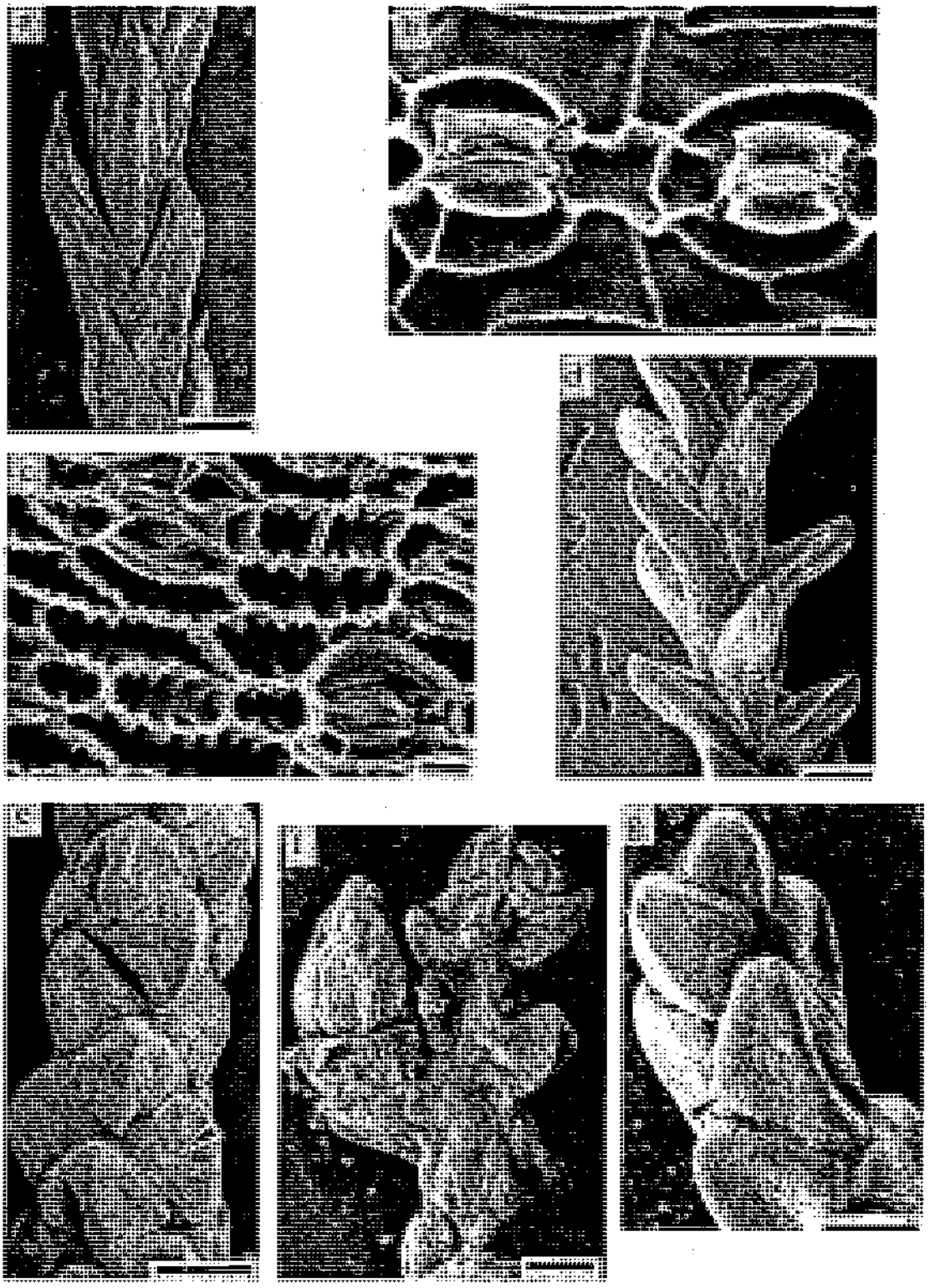


Figure 3.11 : Podocarpaceae : a & b : Extant *Dacrycarpus dacrydioides*. c & d : Extant *Dacrydium cupressinum*. a & d : Leafy stems. b & c : Inner surface of cuticle of adaxial leaf surface. Note the residual of the cutin envelope on the prominent cutin flange (arrow), and the lack of cell wall buttressing in *Dacrycarpus*, and the buttressed cell walls and small cutin flange (arrow) in *Dacrydium*. e, f & g : *Lagarostrobos franklinii*. e & g : Leafy stems. Note the stomata on the abaxial leaf surfaces (arrows). e : Fossil from Regatta Point. f : Fossil ovuliferous cone from Regatta Point. g : Extant leafy stem. Scale bars for a, d, e, f & g = 0.5 mm, for b & c = 10 µm.

***Lagarostrobos franklinii* (ME, RE, RPU1 &2)**

Specimens examined : ME 81-105
RE 4456-5675
RPU 029, 061, 102-108, 111-133, 190, 343, 410, 470, 686-800, 1447-1942

Discussion : This fossil taxon was illustrated in Hill and Macphail (1985) and recorded in Fitzsimons *et al.* (1990) and Jordan *et al.* (1991). Leafy stems (Figure 3.11 e & f) consistent with, and characteristic of *L. franklinii* (Figure 3.12 g) occur in all the sediments studied. The phyllotaxy, leaf and cuticle morphology are all consistent with extant *L. franklinii*, which have been shown to be distinct from all other extant podocarpaceous species based on these characters (Wells and Hill 1989 b). They have tightly appressed leaves which are shorter than most extant forms of *L. franklinii*. The Regatta Point specimens represent the earliest macrofossil record of *L. franklinii*. The absence of macrofossils of this species in the Tertiary is surprising since macrofossils occur abundantly through the Tasmanian Pleistocene, pollen attributed to the species is abundant in many Tertiary macrofossil bearing sediments (Martin in press), and its foliage seems to be very resistant to breakdown. Its foliage appears to be over-represented in riverine litter samples (see chapter 4). Its abundance in Tasmanian macrofossil-bearing Pleistocene sediments may be partly attributed to its riparian habit. Hill (in press) suggests that this sparsity of macrofossils during the Tertiary may be due to the pollen having been produced by one or more closely related species which had significantly different ecology (e.g. they may not have been as riparian as *L. franklinii* tends to be). *Lagarostrobos franklinii* pollen is often over-represented in current pollen samples (e.g. Macphail *et al.* 1991).

Lagarostrobos franklinii is endemic to Tasmania, where it mainly occurs as a rainforest tree, often in riparian situations. It also occurs in one locality, Mt. Read, as subalpine trees, and shrubs (Peterson 1991). It is fire sensitive (Gibson 1986), and it is likely that it may have had a wider distribution in the past and become reduced with higher fire frequencies in the Late Pleistocene (see Chapter 5). It is well dispersed by water, which partly explains its preference for riparian forests but unlike many other

members of the Podocarpaceae it does not have its seeds enclosed in fleshy arils (Shapcott 1991).

***Microcachrys tetragona* (RPU2)**

Specimens examined : RPU 509, 523, 810-842

Discussion : These fossils (Figures 3.13 a, c, e & f) are indistinguishable from extant *Microcachrys tetragona* (Figures 3.13 b & d). The stomatal morphology is characteristic of Podocarpaceae, and the opposite and decussate phyllotaxy is diagnostic of this genus and species among the imbricate-leaved Podocarpaceae (Wells and Hill, 1989 b). Similar phyllotaxy occurs in Cupressaceae, and in particular, in the extant Tasmanian cupressaceous species *Diselma archeri* (Figure 14 a & d). *Diselma archeri* differs from the fossil in having cuticle characters which are typical of the Cupressaceae (epidermal papillae, and more irregular arrangement of the subsidiary cells than in the Podocarpaceae).

Microcachrys tetragona is now restricted to alpine habitats of Tasmania. It is a prostrate shrub which is found spreading across rocky areas, although it appears to require fairly abundant water. It is known, however, to grow in cultivation in much warmer conditions, e.g. at Canberra Botanic Gardens. The seeds are embedded in the bract scale which is fleshy and scarlet when mature (Curtis and Morris 1975) and may be involved in dispersal by birds since birds, particularly green rosellas, can often be seen feeding on the mature cones.

***Phyllocladus asplenifolius* (ME, RE & RPU1)**

Specimens examined : ME 106-110
RE 5676-6709
RPU 015-017, 186-189, 409 & 482

Discussion : This fossil taxon has been illustrated by Hill and Macphail (1985) and Hill (1989) and recorded in Fitzsimons *et al.* (1990) and Jordan *et al.* (1991). The distinctive phylloclades of *P. aspleniifolius* (Figure 3.14 b & e) have been found in all the sediments studied except Regatta Point leaf beds (RPU2). The phylloclades extracted from the sediments are all at the small end of the range of extant *P. aspleniifolius*

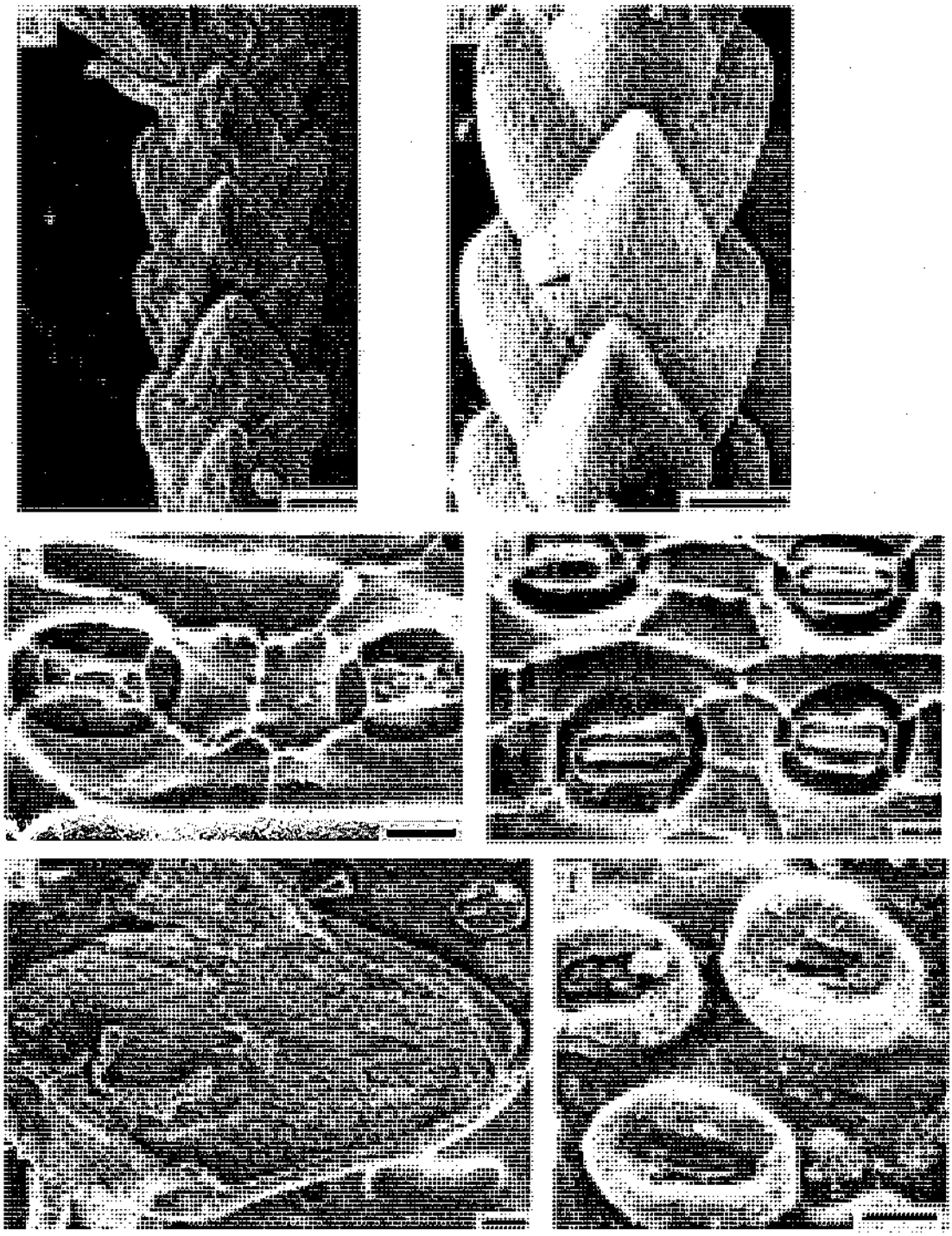


Figure 3.13 : *Microcachrys tetragona*. a, c, e & f : Fossil *M. tetragona* from Regatta Point. a : Leafy stem. Note the opposite and decussate phyllotaxy. c : Inner surface of cuticle of adaxial lead surface showing stomata. e : Adaxial surface of leaf. Note the marginal frill (arrow). f : Outer surface of adaxial leaf surface. Note the florin rings. b & d : Extant *M. tetragona*. b : Leafy stem. Note the similarity in leaf shape and distribution to the fossil, and the marginal frill (arrow). d : Inner surface of cuticle of adaxial leaf surface. Note the similarity to the fossil. Scale bars for a & b = 0.5 mm, for c, d e & f = 10 µm.

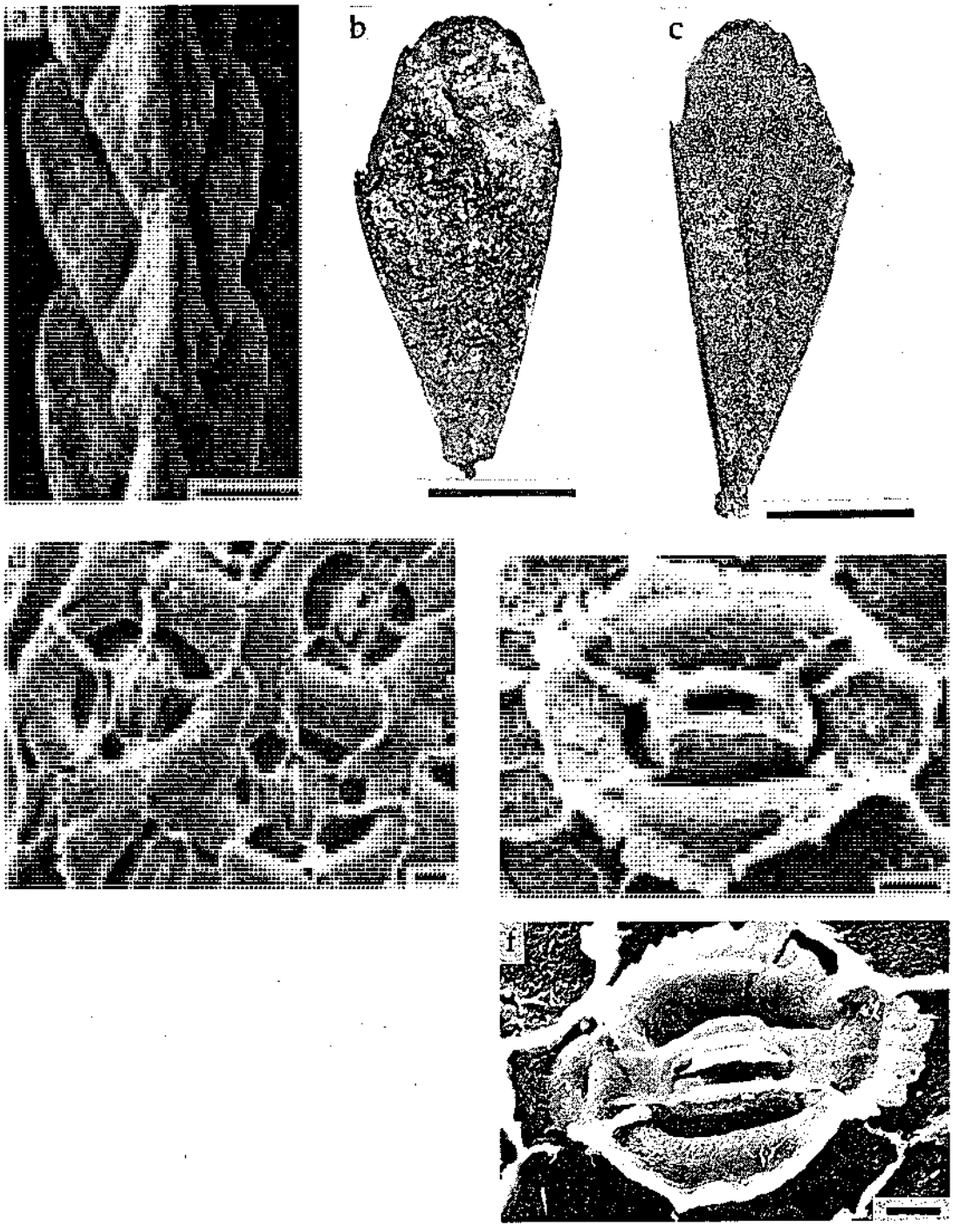


Figure 3.14 : *Diselma archeri* and *Phyllocladus aspleniifolius*. a & d : *Diselma archeri*. Compare with *Microcachrys tetragona* (Figure 3.13). a : Leafy stem. Note the more acute/acuminate leaf shape than *M. tetragona*. d : Inner surface of cuticle of adaxial leaf surface. Note the less regular arrangement of guard cells than in *M. tetragona*, and the epidermal papillae (arrow). b & e : Fossil *P. aspleniifolius* from Regatta Point. c & f : Extant *P. aspleniifolius*. b & c : Phylloclades. e & f : Inner surfaces of cuticle showing stomata. Scale bars for a = 0.5 mm, for b & c = 5 mm, for d, e & f = 10 μm.

(Figure 3.14 c & f) but also lie within the range of *P. alpinus* which is considered by Hill (1989) to be a variant of *P aspleniifolius. Phyllocladus* macrofossils have been found in Tertiary sediments (Hill 1989) and are common in the Quaternary in Tasmania (Hill and Macphail 1985; Fitzsimons *et al.* 1990; Colhoun *et al.* 1989).

Phyllocladus has had a wider distribution than at present : its pollen is known from south-eastern mainland Australia and north-east Queensland (Kershaw 1984, 1985) from the Late Pleistocene. The presence of *Phyllocladus* pollen in Holocene sediments in Victoria (Churchill and Dodson 1980) may have been the result of long distance dispersal from Tasmania, or possibly New Zealand (Head 1985). *Phyllocladus aspleniifolius* is endemic to Tasmania where it occurs in rainforest and other wet forest from lowland to subalpine areas and rarely in alpine areas, and *P. alpinus* occurs in cooler parts New Zealand, particularly in subalpine shrubberies. The seeds are enclosed in fleshy arils which may be involved in dispersal by birds.

***Podocarpus* cf. *lawrencii* (RPU1)**

Specimens examined : RPU 018-021,328, 361, 414 & 491

Discussion : This taxon (Figures 3.15 a, b, e & g) was included in Hill and Macphail (1985). The leaves are longer, more acute and more falcate than is usual in *P. lawrencii* (Figure 3.13 c) but the differences do not seem sufficient to separate the fossils from this extant species. The cuticle morphology lies within the range of extant *P. lawrencii* (Figure 3.13 d, f & h). *Podocarpus* is a very large genus, with many species of subgenus *Podocarpus* having leaves and cuticles similar morphologically to these fossils. There is no reliable published record of *Podocarpus* macrofossils from Tasmania, but leaves attributable to the genus occur in the Oligocene Cethana sediments (Carpenter 1991). *Podocarpus lawrencii* occurs mainly as a low shrub in rocky areas of subalpine Tasmania, but also occurs as a tree in apparently relictual patches in lowland Tasmania, and as a tree or tall shrub in sub-alpine areas of south-eastern Australia. *Podocarpus* subgenus *Podocarpus* species with similar leaf size to the fossils occur in wet forests and wet sub-alpine and alpine areas in New Zealand and

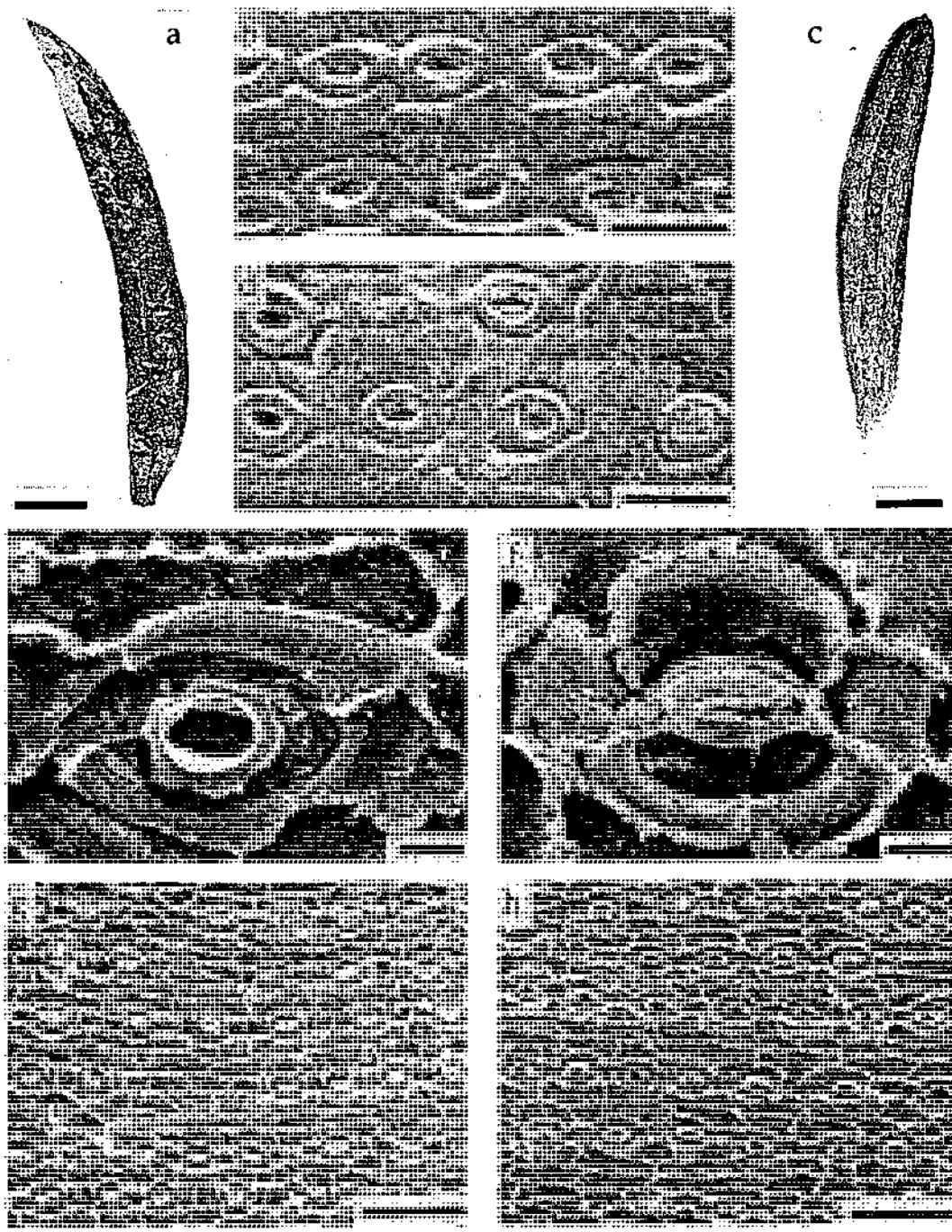


Figure 3.15 : *Podocarpus*. a, b, e & g : Fossil *P.* cf. *lawrencii* from Regatta Point. c, d, f & h : Extant *P. lawrencii*. a & c : Leaves. Note the more acute, falcate leaf shape of the fossil than the extant leaf. b & d : Outer surface of stomatiferous leaf surface. Note the elevated cutin rings around the stomatal aperture (Florin rings). e & f : Inner surface of the cuticle of the stomatiferous leaf surface. Note the more elongate stomatal complex in the fossil than the extant cuticle. g & h : Inner surface of the cuticle of the stomatiferous leaf surface. Note the buttressed cell walls, and the distribution of stomata in about 6 lines. One of these bands of about six lines of stomata occurs on each side of the midrib. Scale bars for a & c = 2 mm, for b & d = 50 µm, for e & f = 10 µm, for g & h = 100 µm.

Australia. The seeds of these *Podocarpus* species are usually solitary on short shoots and are subtended by red fleshy bracts (Curtis and Morris 1975) which may favour dispersal by birds.

Taxodiaceae

***Athrotaxis selaginoides* (RE)**

Specimens examined : RE 7820-8052

Discussion : Fitzsimons *et al.* (1990) recorded the presence of this taxon. Leafy stems indistinguishable from extant *A. selaginoides* occur in the Regency sediments (Figures 3.16 c & d). *Athrotaxis selaginoides* (Figure 3.17 a & d) now occurs in moderate altitude forest to alpine shrubbery in Tasmania.

***Athrotaxis* cf. *laxifolia* (RPU1&2)**

Specimens examined : RPU 007, 014, 026, 035, 036, 060, 062, 134-166, 225-229, 232, 235, 238, 412, 437, 451, 460, 474, 481, 843-900

Description : Leaves imbricate but slightly spreading, ovate-lanceolate, thick, keeled, apex acute, more or less incurved, 3 - 5 mm long, 1.2 - 1.6 mm broad. Cuticle with vestigial marginal frill near apex, epidermal cells rectangular, ± in lines, stomata in dense bands in basal 1/3 of leaf either side of keel abaxially, in dense bands either side of midleaf adaxially, subsidiary cells 5 or 6, radial, often shared. Seed cones ± spherical, about 1.2 cm in diameter. Cone scales about 15, broad, thick, tapering towards the base. Ovuliferous scales much reduced, fused to adaxial surface of bract scale. Bract scales broadly ovate, abruptly curved adaxially to cover ovuliferous scale, extended distally to form a thin, acute, keeled flap, imbricate with other bract scales.

Discussion : This taxon was described and illustrated in Hill and Macphail (1985) as two taxa, *A. selaginoides* and *A.* cf. *cupressoides*, but examination of a large number of specimens suggests that they are best described as a single, possibly extinct, taxon. Abundant fossil leafy stems (Figure 3.16 a) and occasional cones (Figure 3.16 b) of *Athrotaxis* occur in the Regatta Point sediments. *Athrotaxis* is endemic to Tasmania with three species, two of which are common

 : *A. selaginoides* (Figure 3.17 a) and *A. cupressoides* (Figure 3.17 c). It has been suggested that the third species, *A. laxifolia* (Figure 3.16 b), is a hybrid between these two species, since its morphology seems to be intermediate between the other two species in all aspects. Its distribution is consistent with this hypothesis since it is only known to occur with either *A. selaginoides* or *A. cupressoides*, although populations of significant size occur in the mountains near Tasmania's west coast (e.g. on Mt. Read).

The cone scales of *Athrotaxis* are characterised by the bract scale and ovuliferous scale being fused, with the apex of the bract scale forming a thin triangular protuberance (Florin 1951). In *A. selaginoides* the ovuliferous scales are much reduced and entirely covered by the bract scales, and the protuberances are large and curved towards the cone apex and overlap the upper cone scales. In *A. cupressoides* the ovuliferous scales are approximately equal to the bract scales, and fused together to form peltate cone scales. The bract scale protuberances of *A. cupressoides* are small scales near the middle of the peltate cone scales forming the surface of the cone. The cones of *A. laxifolia* are variable but seemingly intermediate to those of the two other extant species, with both ovuliferous and bract scales well developed, and forming a peltate structure. The cone scales of the fossil species show strong reduction of the ovuliferous scales, and the bract scale protuberance is prominent and overlaps the other cone scales, and hence is similar to *A. selaginoides.* This protuberance is, however, shorter in the fossil. The cones are distinctly smaller than those of *A. selaginoides* and smaller than most *A. laxifolia* cones.

There is variation in the vegetative morphology of the fossils, but some generalizations can be made. The leaves of the fossils are smaller, and more appressed than those of *A. selaginoides.* The leaf morphology of the fossil is clearly distinct from *A. cupressoides* which has smaller, relatively broader, more appressed leaves, with prominent marginal frills. Its leaf morphology is similar to some forms of *A. laxifolia.* There is little variation in cuticular morphology between the extant species of *Athrotaxis* (Figure 3.17 d) and the fossils, but the stomatal form is diagnostic of the genus. The cones have foliage attached, which is consistent with all the vegetative

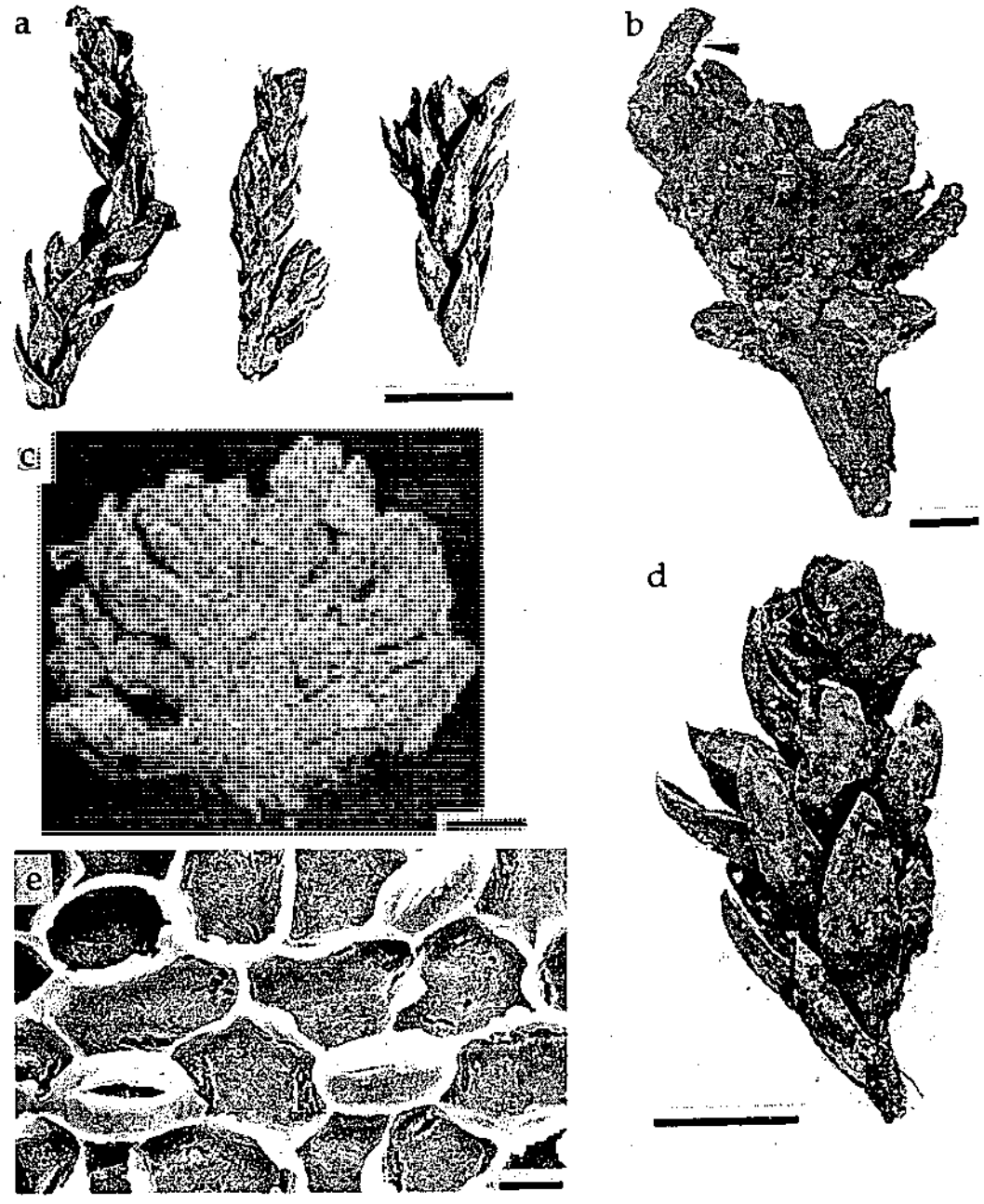


Figure 3.16 : Fossil *Athrotaxis*. a, b & e : Fossil *Athrotaxis* cf. *laxifolia* from Regatta Point. a : Leafy stems showing the variation in form. Note the smaller leaf size, and generally more appressed leaves than in Figure 3.17 a, and narrower leaves than in Figures 3.17 b & c. b : Ovuliferous cone (probably immature). Note the apically pointing bract scale protuberance (arrow). e : Inner surface of cuticle of adaxial leaf surface. Note the stomatal form with scarcely differentiated subsidiary cells similar to Figure 3.17 d. c & d : Fossil *A. selaginoides* from Regency. c : Ovuliferous cone (probably immature). Note the apically pointing bract scale protuberance (arrow). d : Leafy stem. Note the similarity in leaf size and shape to extant *A. selaginoides* (Figure 3.17 a). Scale bars for a & d = 5 mm, for b & c = 1 mm, for e = 10 µm.

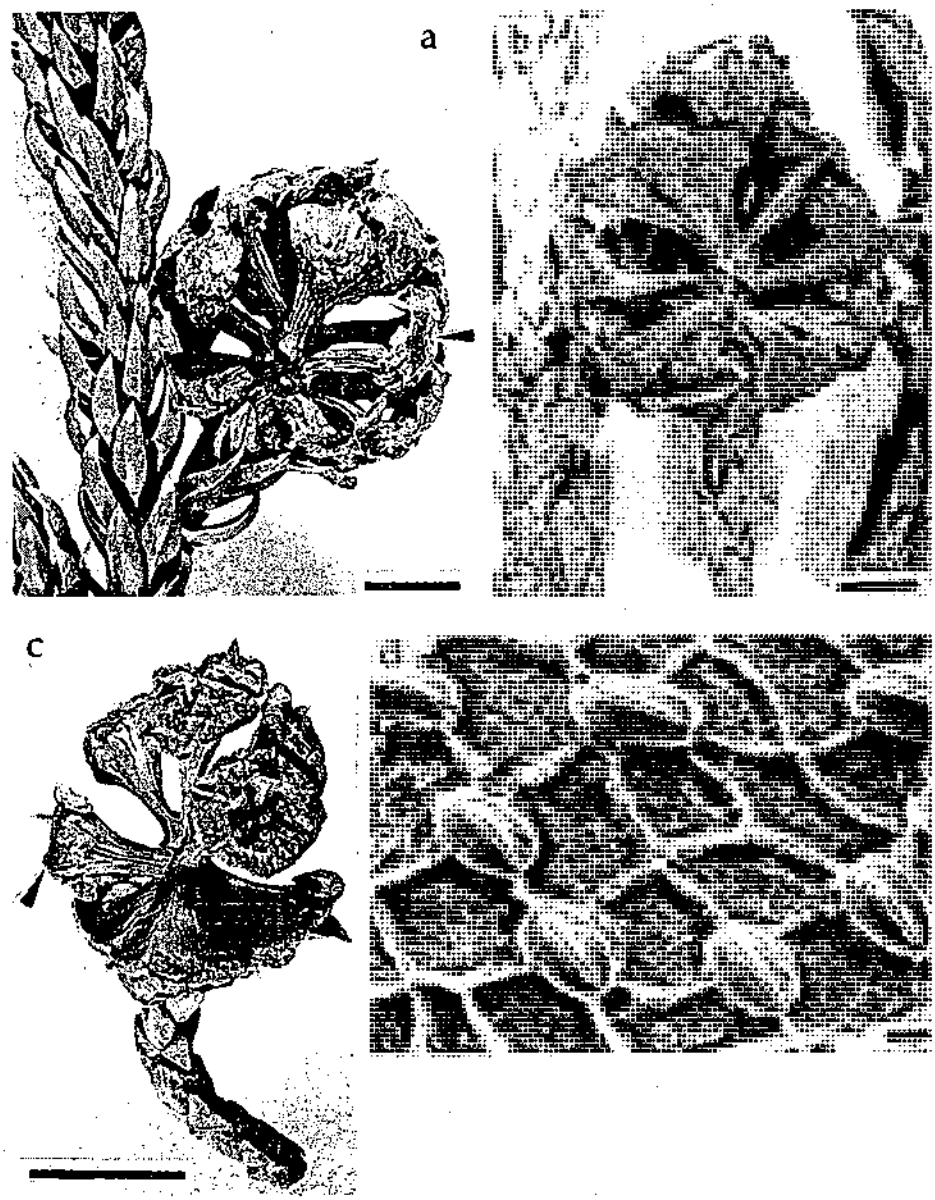


Figure 3.17. Extant *Athrotaxis* : a, b & c : Leafy stems and ovuliferous cones. a : *A. selaginoides*. a : Note the spreading leaves and apically pointing large protuberance of the bract scales (arrow). b : *A. laxifolia*. Note the slightly spreading, small leaves and the bract scale/ovuliferous scale complexes (arrow) intermediate in form between *A. selaginoides* and *A. cupressoides*. c : *A. cupressoides*. Note the appressed, small leaves and the peltate bract scale/ovuliferous scale complexes (arrow), with the protuberance on the distal surface. d : Inner surface of cuticle of adaxial leaf surface of *A. selaginoides*. Scale bars for a, b & c = 5 mm, for d = 10 μm.

fragments of *Athrotaxis*.

The fossils are therefore similar to *A. selaginoides*, but fall outside the morphological range of this species. Stem fragments of *Athrotaxis* species found in contemporary litter fall within the morphological ranges shown in herbarium specimens of the relevant species. The distinctiveness of the fossils cannot therefore be attributed to collection bias in herbarium specimens, or to taphonomic bias. The fossils fall within the broad range of *A. laxifolia*. There is, however, a problem in interpreting the fossils as *A. laxifolia*. *Athrotaxis laxifolia* always occurs in association with either *A. cupressoides* or *A. selaginoides*. There is no evidence of the presence of either of these taxa at Regatta Point. Trees of *A. laxifolia* which are similar to the fossils only occur in the large western Tasmanian populations of *A. laxifolia*, where a wide range of forms of the genus occur. In these and all other extant populations of *A. laxifolia* the majority of trees have morphology which appears to be strictly intermediate between *A. cupressoides* and *A. selaginoides*. These forms have more appressed and less elongate leaves than the fossils, and have more reduced bract scales than the fossils. The fossils therefore came from a populations of a species which is unlike any extant population of *A. laxifolia*. The fossils are therefore from a genus which is extant in Tasmania, and may be an extinct species, or may be *A. laxifolia*.

The extant species of *Athrotaxis* are trees of alpine, subalpine and moderate altitude forest of western and southern Tasmania. They are dependant on high light conditions for regeneration, and appear to require some form of low frequency disturbance. (Cullen 1987 a; Cullen and Kirkpatrick 1988). They are poorly dispersed, with dry winged seeds which are rarely dispersed more than about three times the diameter of the tree (Cullen 1987 b).

3.3.4 : Angiospermae

Casuarinaceae

The infructescences of Casuarinaceae are woody cone like structures made up of several longitudinal rows of fruit, each of which is made up of a single seed held between two thick woody bracteoles subtended by a

single bract (Johnson and Wilson 1989). In *Allocasuarina* each bracteole has a scale like protuberance associated with it. Figures 3.18 e & f show these structures in *A. verticillata* and *A. zephyrea*. The photosynthetic organs are stems with highly reduced whorled leaves (or whorled leaves almost entirely fused along the stem) (see Figure 3.19).

Both pollen and macrofossils of Casuarinaceae are prominent in the Cainozoic fossil record of Australia. Species of *Allocasuarina* occur in a wide range of dry or nutrient deficient habitats. *Allocasuarina* species are poorly dispersed with winged seeds which are relatively massive, and unlikely to be transported far by wind. There is, however, evidence that *Allocasuarina* may have occurred in a wider, or different range of habitats during the Pleistocene (see Chapter 6).

***Allocasuarina zephyrea* (ME), *A. ?zephyrea* (RE)**

Specimens examined : ME 638-1255
RE 7548-7819

Discussion : Jordan *et al.* (1991) illustrate this taxon from the Melaleuca Inlet sediments. Fitzsimons *et al.* (1990) record the presence as Casuarinaceae in the Regency sediments. The fossil cones (Figure 3.18 c) and stems (Figure 3.19 a) from the Melaleuca sediments are indistinguishable from extant *A. zephyrea* (Figures 3.18 d & 3.19 b) which is now common and widespread in western Tasmania in sedgeland-heath communities, from lowland to lower alpine areas. The stems found in the Regency sediments are consistent with *A. zephyrea*, but are also consistent with some other extant species of *Allocasuarina* e.g. *A. littoralis*.

***Allocasuarina* cf. *verticillata* (RPU 1&2)**

Specimens examined : RPU 008, 030, 033, 034, 037, 167-185, 224, 239, 248, 322-325, 347, 363, 404, 450, 455, 463, 467, 480, 910-1030

Description : Foliage articulate. Articles 7 - 14 mm long, about 0.8 mm broad, terete, phyllichnia flat or slightly angular, teeth acute, usually 9, erect, 0.8 - 1 mm long. Stomata in 3 - 5 longitudinal rows on either side of groove, guard cells transverse to axis of article, with two roughly equal lateral subsidiary cells and separated by one or more other epidermal cell. Cuticle of phyllichnia with rectangular cells longer than broad near groove,

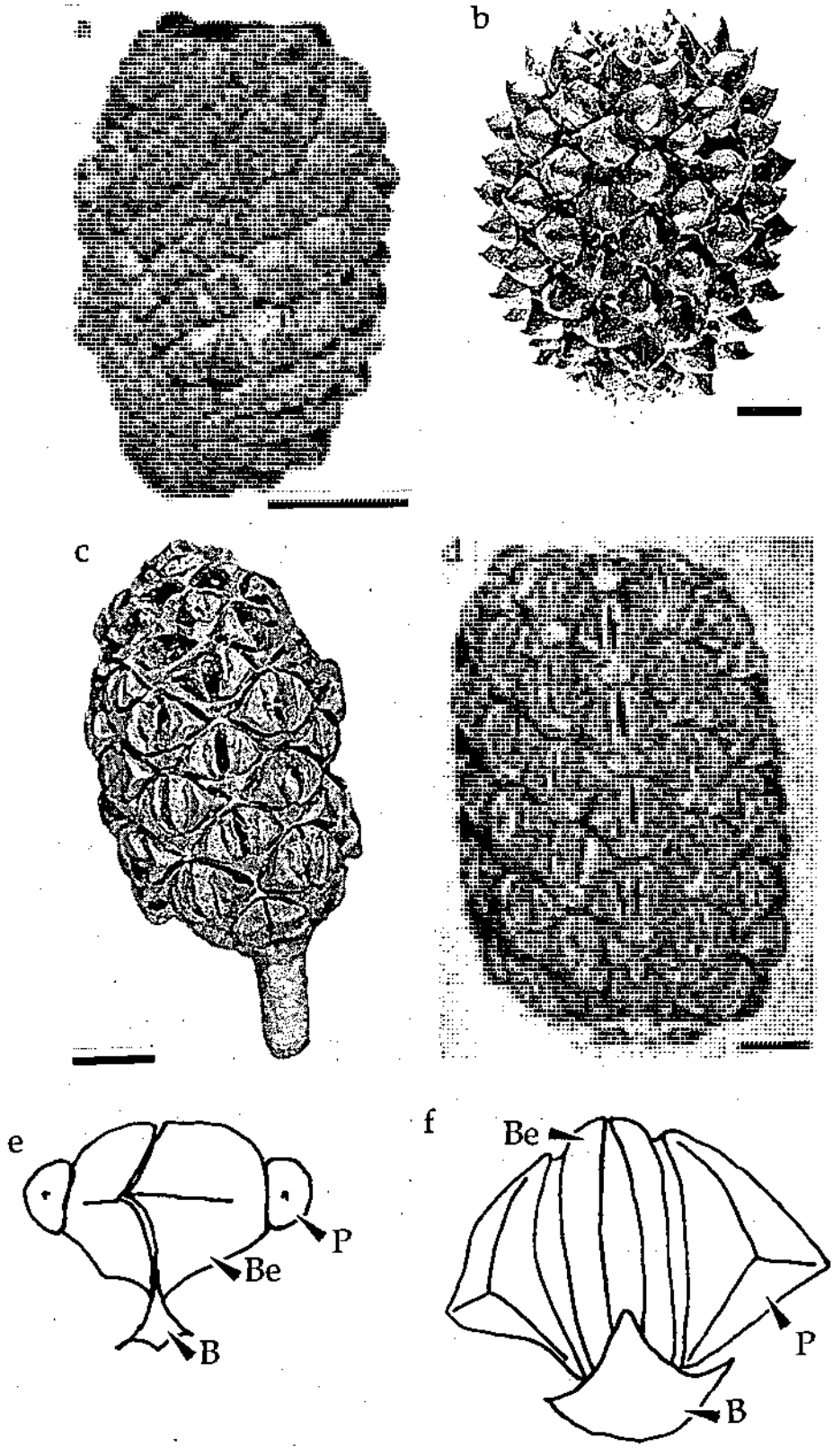


Figure 3.18 : *Allocasuarina* Infructescences. a : Fossil *Allocasuarina* cf. *verticillata* from Regatta Point. Note the massive bracteoles, and tiny free dorsal protuberances. b : Extant *A. verticillata.* c : Fossil *A. zephyrea* from Melaleuca Inlet. d : Extant *A. zephyrea.* Note the pyramidal dorsal protuberances in this and the fossil cone from Melaleuca. Scale bars = 5 mm. e & f : Fruiting complexes of *Allocasuarina* illustrating the bracts (B), bracteoles (Be) and dorsal protuberances (P). e : Extant *A. verticillata.* f : Extant *A. zephyrea.*

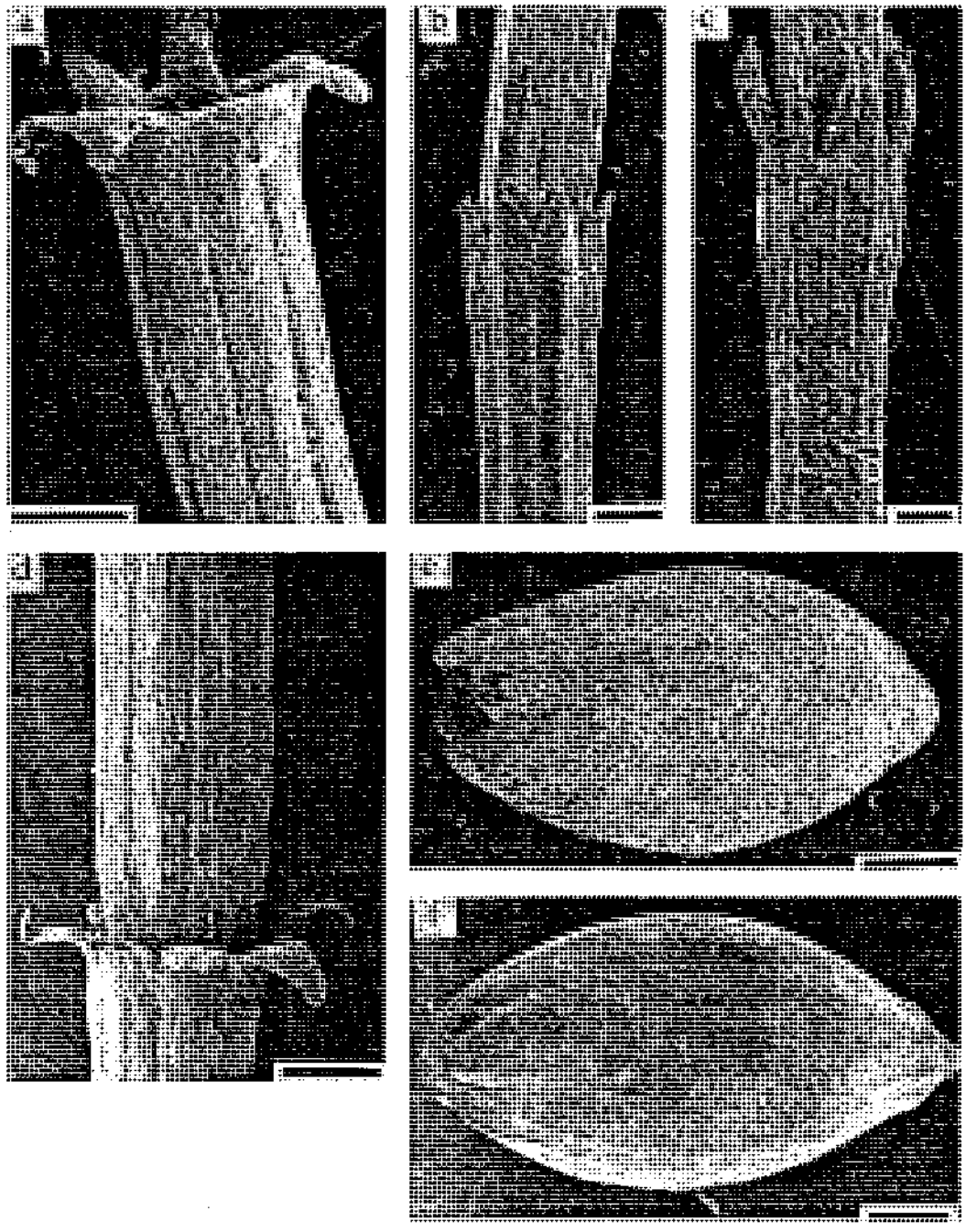


Figure 3.19 : *Allocasuarina* and *Gahnia*. a, b, c & d : Photosynthetic stems of *Allocasuarina*. a : Fossil *A. zephyrea* from Melaleuca Inlet. b : Extant *A. zephyrea*. c : Extant *A. verticillata*. Note the verrucae on the stem (arrow), which are absent from the Regatta Point fossils. d : Fossil *Allocasuarina* cf. *verticillata* from Regatta Point. e & f : *G. grandis* seeds. e : Fossil *G. grandis* from Melaleuca Inlet. f : Extant *G. grandis*. Scale bars = 0.5 mm.

uniformly broader than long and thick walled towards middle. Infructescences shortly pedunculate, cylindrical to barrel shaped, 12 -16 mm long, 10 - 14 mm broad, with 18 - 22 longitudinal rows of fruit, bracts small, acute, bracteoles prominent, thickened, broadly acute, with distally curved mucro, protuberance small, acute, mucronate, more or less free of the bracteole.

Discussion : Hill and Macphail (1985) illustrate this taxon and justify its identification as *Casuarina* sensu lato, but this study refines the identification to *Allocasuarina* and probably an extinct species. The other three genera of the Casuarinaceae (*Casuarina*, *Gymnostoma* and *Ceuthostoma*) have much less thickened bracteoles and no dorsal protuberances (Johnson and Wilson 1989). The fruit complex with small, acute, more or less free dorsal protuberances, associated with very thick bracteoles is diagnostic of *Allocasuarina* section *Oöpitys* which contains the extant species *A. verticillata* (Figure 3.18 b), which is widespread in eastern Australia including Tasmania, and *A. huegeliana*, which is restricted to Western Australia. The bracteoles in *A. huegeliana* differ from the fossil in being obtuse and much more massive. The fossil (3.18 a) also has smaller cones than *A. huegeliana*. The fossil infructescences fall outside of the range of mature *A. verticillata* infructescences only in their size, which are 15-30 mm x 12-15 mm in *A. verticillata*, and in having more prominent bracts. The fossil infructescences are not unlike immature infructescences of *A. verticillata*. However many infructescences of this size range occur in the sediments, and none smaller or larger except for very immature forms (see Figure 3 in Hill and Macphail (1985)). Many more mature fruit than immature fruit of *A. verticillata* can be found in the litter underneath trees of this species and hence the occurrence only of immature forms in sediments is very unlikely, unless there is preferential preservation of these forms. Mature cones of *A. verticillata* do not appear to differ in their ability to float or sink from immature cones, except that they float when dry.

The fossil stem articles (Figure 3.19 d) are consistent with *A. verticillata* (Figure 3.19 c) in diameter (mostly >1 mm), and in the number of teeth (mostly 9 in the fossils). However, the articles in the fossils (7 -14 mm) are shorter than those of *A. verticillata* (15 -20 mm) and in the cuticles differ : the

ribs between stomatal grooves in *A. verticillata* and *A. huegeliana* are verrucose (Figure 3.19 c) and this is expressed in the cuticle by roughly round areas of cuticle with thick cell walls, whereas the fossils have broad continuous bands of thick walled cells down the centre of the rib, which makes them quite similar to other taxa including *A. rigida*.

Figure 3.20 : Extant distribution of *Allocasuarina verticillata*.

There are no fossil stem fragments consistent with *A. verticillata* in the sediments but there are abundant (>1800) well preserved stem fragments of the form described above. All the fossil infructescences are consistent with being from one species. *Allocasuarina* stems are likely to be easily preserved, since they are highly sclerophyllous and small. The abundant occurrence of the genus in most macrofossil bearing Pleistocene sediments in Tasmania also suggests that it is relatively easily preserved. Both infructescences and stems occur together in several clasts of the RPU1 sediments containing distinct floras, and sediments of different texture from sandy to homogeneous siltstone. Taphonomic conditions which would allow the preservation of only stem fragments of one species, and only

cones of another are unlikely to be preserved through changes of both source vegetation and depositional environment. It seems highly unlikely, therefore, that abundant stems of one species of *Allocasuarina* would occur with frequent infructescences of another species without the occurrence of at least some stems of the second species. It is probable that the *Allocasuarina* stems and infructescences are of the same species. The fossils would then be a globally extinct species.

Allocasuarina verticillata is a small tree which occurs in woodlands and sclerophyll forests of Tasmania, and other areas of south-eastern Australia (Figure 3.20). It is most common in areas with relatively low fire frequencies e.g. along the tops of sea cliffs, or in sheltered gullies that are too dry to support wet sclerophyll forest.

Cunoniaceae

***Anodopetalum biglandulosum* (ME)**

Specimens examined : ME 111-115

Discussion : Jordan *et al.* (1991) illustrate this fossil taxon. These fossils (Figures 3.21 a, c & e) are indistinguishable from extant *Anodopetalum biglandulosum* (Figures 3.21 b, d & f) which is now common in western Tasmanian rainforests and wet scrub and occasionally extends into alpine areas. The fossils have similar leaf size and cuticle to *A. biglandulosum* growing near the summit of Mt. Read (1140 m a.s.l.) in western Tasmania. The extant cuticles illustrated are lowland forms of the species, which tend to have cells with sinuous walls.

***Bauera rubioides* (ME)**

Specimens examined : ME 116-399

Discussion : Jordan *et al.* (1991) illustrate this fossil taxon. The fossils (Figures 3.22 a, c & e) are indistinguishable in leaf form and cuticle from extant *B. rubioides* (Figures 3.22 b, d & f) which is now common and widespread in western Tasmania in sedgeland-heath, scrub and wet sclerophyll forest communities, from lowland to lower alpine areas. It is a shrub forming tangled masses up to several metres high and is very common on stream banks.

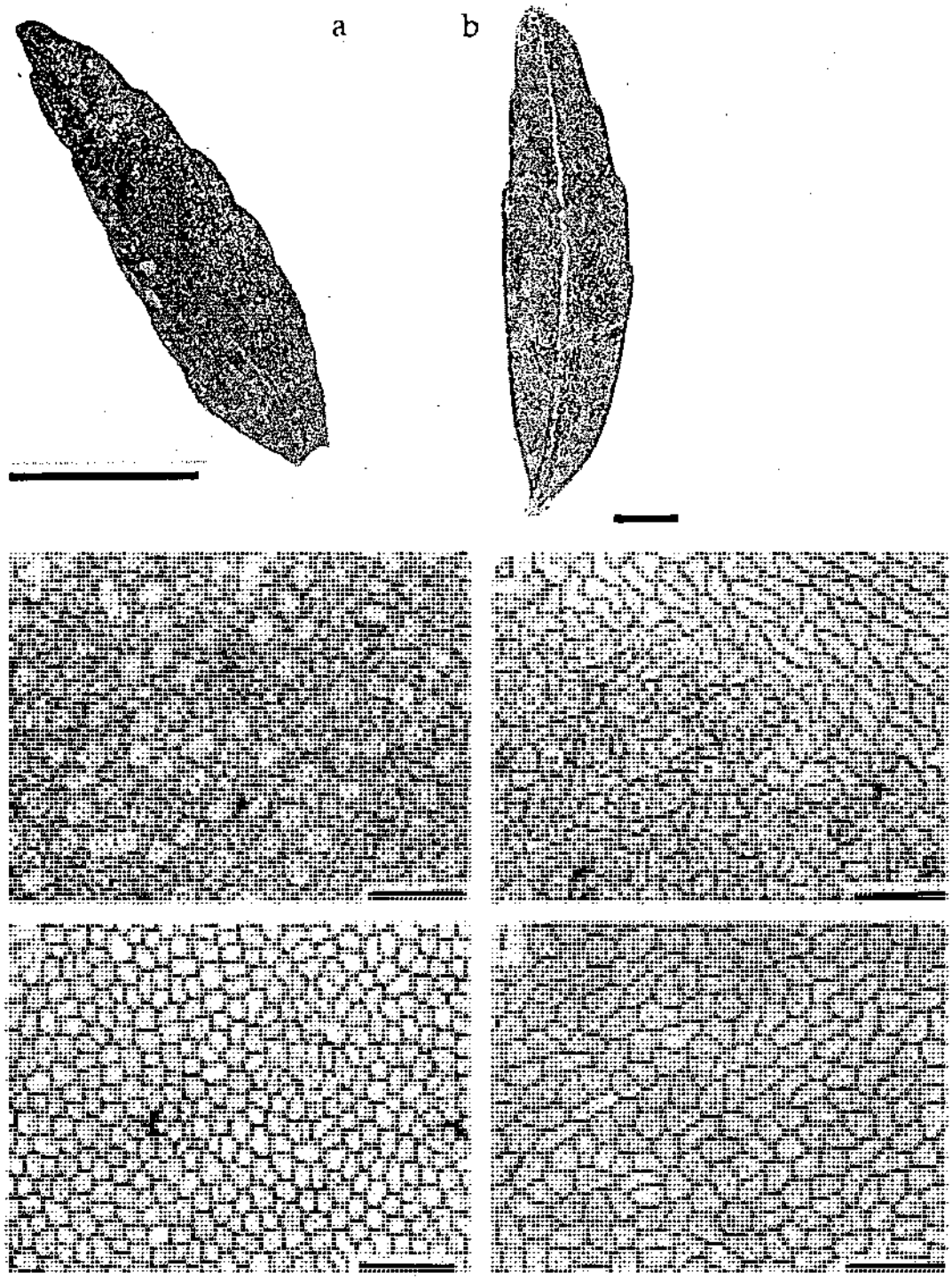


Figure 3.21: *Anodopetalum biglandulosum*. a, c & e : Fossils from Melaleuca Inlet. b, d & f : Extant *A. biglandulosum*. a & b : Leaves. c & d : Cuticle of stomatiferous surface. e & f : Cuticle of non-stomatiferous surface. Scale bars for a & b = 2 mm, for c, d, e & f = 100 µm.

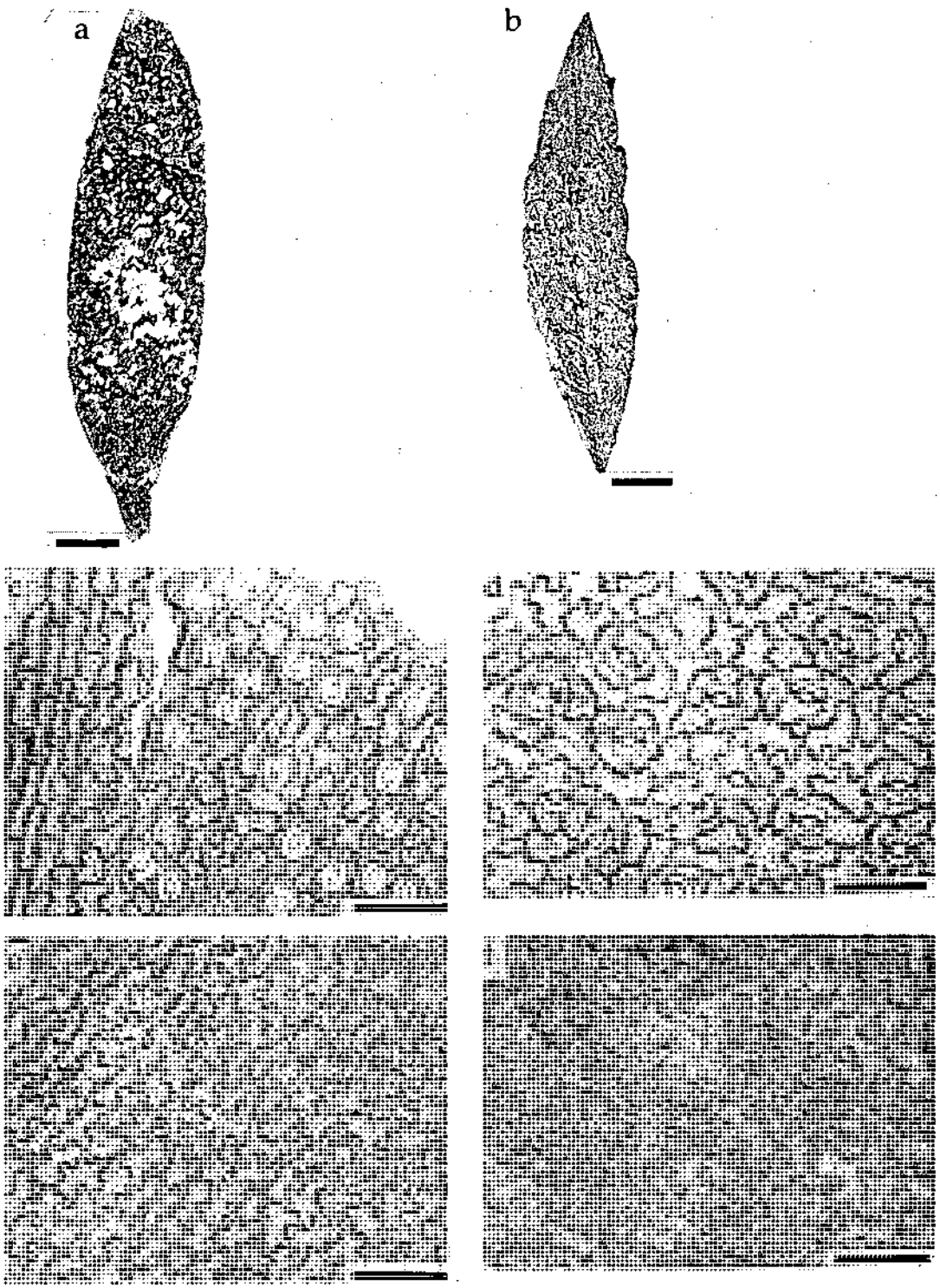


Figure 3.22 : *Bauera rubioides*. a, c & e : Fossils of *B. rubioides* from Melaleuca Inlet. b, d & f : Extant *B. rubioides*. a & b : Leaves. c & d : Cuticle of stomatiferous surface. e & f : Cuticle of non-stomatiferous surface. Scale bars for a & b = 1 mm, for c, d, e & f = 100 µm.

Cyperaceae

***Gahnia grandis* (ME)**

Specimens examined : ME 400-445

Discussion : Jordan *et al.* (1991) illustrate this fossil taxon. These fossil seeds (Figure 3.19 e) are indistinguishable from extant *G. grandis* (Figure 3.19 f). *Gahnia grandis* is now common in scrub and wet sclerophyll forest communities in Tasmania and is generally associated with fire disturbance. It forms large tussocks up to two or three metres high and several metres in diameter and can form virtually impenetrable thickets after fire with *Bauera rubioides*, *Leptospermum* spp. and sometimes *Calorophus elongatus*.

Epacridaceae

The fossil record of the Epacridaceae is poor. Macrofossils have been recognised from the Middle and Late Pleistocene in Tasmania (e.g. from the Regency Interglacial (Fitzsimons *et al.* 1989)). There are no published records of Tertiary macrofossils of Epacridaceae from Tasmania, although many leaves from the very small leaved Monpeelyata assemblage are likely to be from this family (Hill and Gibson 1986 b). The distinctive parallel venation of the leaves and distinctive cuticles allow for reasonably ready identification of Epacridaceae fossils, although the cuticle is often not preserved or only poorly preserved. The cuticles of the Ericaceae and the Epacridaceae, except most of the tribe Styphelidae, have highly sinuous cell walls and distinctive stomata aligned with the long axis of the leaf (e.g. Figures 3.23 e & 3.25 f), in rows parallel to the long axis of the leaf. The Styphelidae, except *Trochocarpa* (e.g. Figure 3.27 f) (which appears to be primitive within the group and has cuticle similar to other epacrids) do not have highly sinuous cell walls of the abaxial surface, but do have stomata in bands bearing distinctive short trichomes (e.g. Figure 3.26 d). Tribe Richeae have cuticles with cell walls so sinuous that they appear superficially like thick ornamented walls (e.g. Figure 3.25 f). The Epacridaceae (except *Prionotes cerinthoides* and the closely related South American genus *Lebetanthus*) have parallel venation, whereas the Ericaceae have reticulate venation. Without cuticular preservation some epacrid leaves may be easily

confused with some Myrtaceae with three or five more or less parallel veins and similar leaf shape (e.g. *Leptospermum scoparium* - Figure 3.46 e). The Styphelidae, which includes *Cyathodes*, *Monotoca* and *Trochocarpa* have fleshy fruit and may be bird dispersed. The other members of the Epacridaceae have capsules and dry seeds which are less likely to be well dispersed.

Tribe Epacridae

***Epacris heteronema* (ME); *E.* ? *heteronema* (RE&RPU1)**

Specimens examined : ME 446-486
RE 8150-8200
RPU 364, 388, 399, 418, 1043-1052,
1043-1052

Discussion : Jordan *et al.* (1991) justify the identification of and illustrate *E. heteronema* in the Melaleuca sediments. These fossils have cuticle (Figure 3.23 d) and leaf form (Figure 3.23 a) which indicate membership of the Epacridaceae. The leaves of extant *E. heteronema* (Figure 3.23 c & e) are highly variable within populations and even on single plants. Some of the leaf forms found in the Melaleuca sediments cannot be readily distinguished from other species of *Epacris*, but forms with truncate leaf bases are characteristic of *E. heteronema*. The sediments contain a wide range of forms typical of modern *E. heteronema* including the diagnostic forms. Fossil leaves from the Regency and Regatta Point sediments (Figure 3.23 b) are also consistent with *E. heteronema*. *Epacris heteronema* is now common in sedgeland-heath in south-west Tasmania, from lowland to subalpine areas.

***Epacris* sp. 1(RPU1)**

Specimens examined : RPU 387

The leaf shape of this fossil (Figure 3.24 a) is consistent with *E. heteronema*, but it is larger than extant forms of that species. *Epacris* species are widespread in Tasmania and elsewhere. This fossil is probably from a species which is extinct in Tasmania.

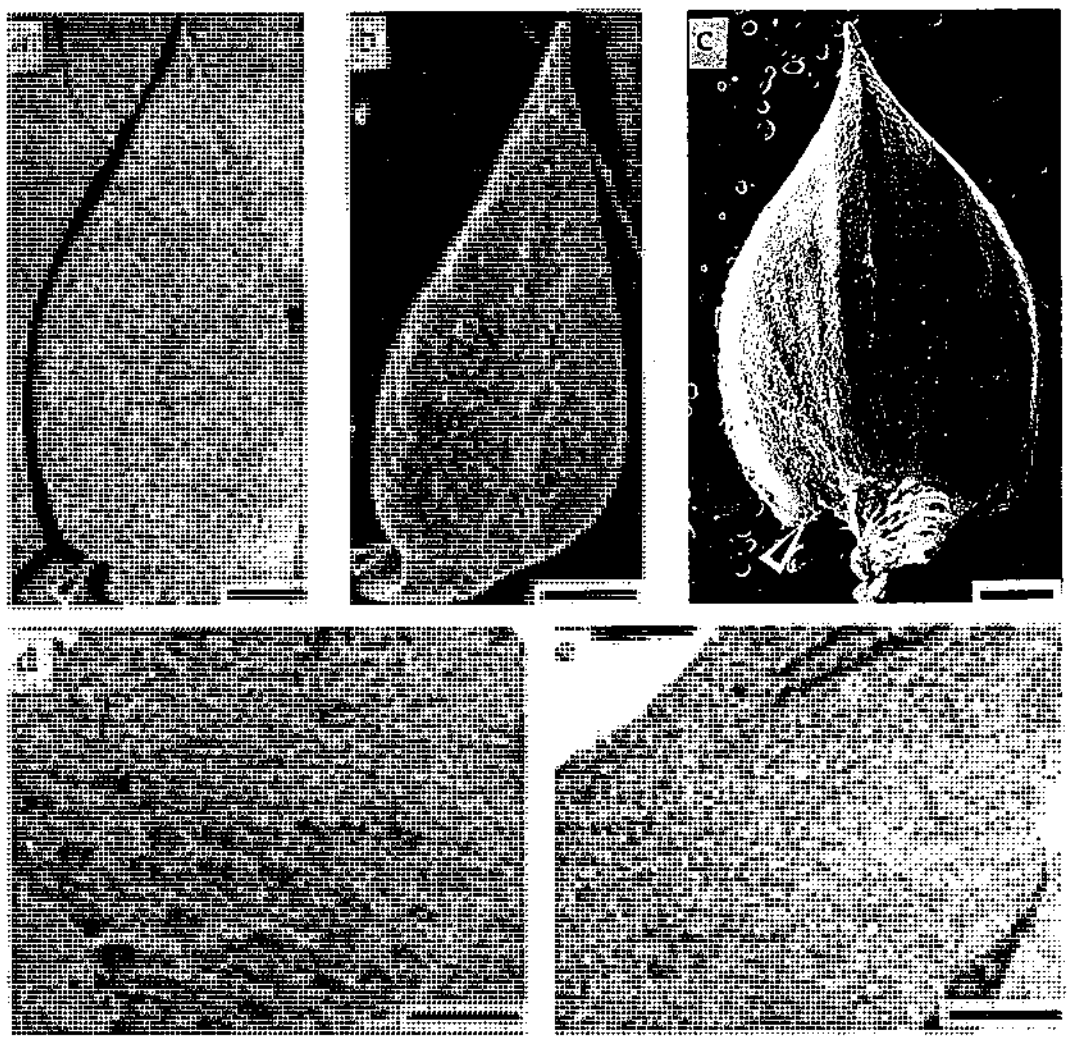


Figure 3.23 : *Epacris*. a & d : Fossil *Epacris heteronema* from Melaleuca. b : Fossil *E.* ? *heteronema* from Regatta Point. c & e : Extant *E. heteronema*. a, b & c : Leaves. The arrows indicates the truncate leaf bases. d & e : Cuticles of stomatiferous surfaces. Note the alignment of stomatal axes, and sinuous cell walls. Scale bars for a, b & c = 0.5 mm, for d & e = 100 µm.

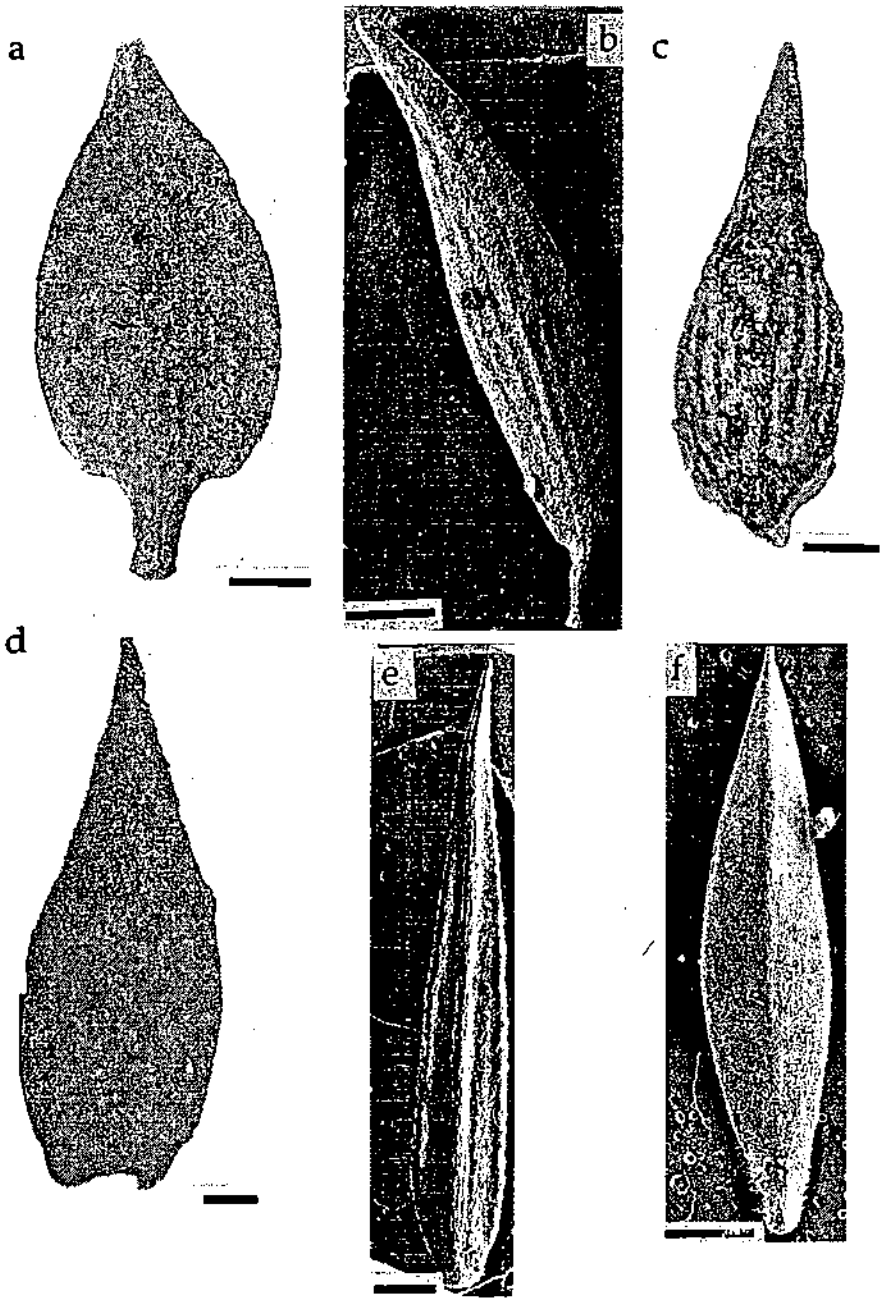


Figure 3.24 : *Epacris* leaves. a : Fossil *Epacris* sp.1 from Regatta Point. b : Fossil *Epacris* sp. 2 from Regatta Point. c & d : Fossil aff. *Epacris* species from Melaleuca Inlet. e : Extant *E. impressa*. f : Extant *E. lanuginosum*. Scale bars for a, b, e & f = 1 mm, for c & d = 0.2 mm.

***Epacris* sp. 2 (RPU1&2)**

Specimens examined : RPU 1053-1069

Discussion : This taxon (Figure 3.24 b) has linear lanceolate leaves similar to several species of *Epacris* (e.g. Figure 3.24 e & f).

aff. *Epacris* species (ME)

Specimens examined : ME 487-496

Jordan *et al.* (1991) illustrate these taxa. Other probable *Epacris* leaves occur in the Melaleuca Inlet sediments (Figures 3.24 c & d) that cannot be identified to species level. Species with leaves similar to these now occur widely in Tasmania.

Tribe Richeae

aff. *Richea milliganii* / *R. acerosa* (RPU1&2, RE)

Specimens examined : RPU 349, 360, 386, 394, 423, 473, 1070-092
RE 8221-8249

Discussion : This elongate triangular leaf (Figure 3.25 a) from the Regatta Point sediments with numerous parallel veins and a sheathing base, has cuticle which shows affinity with tribe Richeae. The fossil is like *R. milliganii* (Figure 3.25 b) and *R. acerosa* and unlike other extant Tasmanian species of *Richea* or *Dracophyllum* in having a relatively narrow, and apparently straight leaf. *Richea acerosa* and *R. milliganii* are shrubs of subalpine areas of Tasmania. Leaves consistent in form and cuticle morphology with *Richea* also occur in the Regency sediments.

Other species of *Richea* and *Dracophyllum* occur in a wide range of well watered habitats in Tasmania and elsewhere, but are most common in subalpine or alpine areas.

***Sprengelia incarnata* (ME)**

Specimens examined : ME 502-514

Discussion : Jordan *et al.* (1991) illustrate this taxon. These leafy inflorescences (Figure 3.25 c & e) are indistinguishable from extant *S. incarnata* (Figure 3.23 d & f) which is now widespread and common in

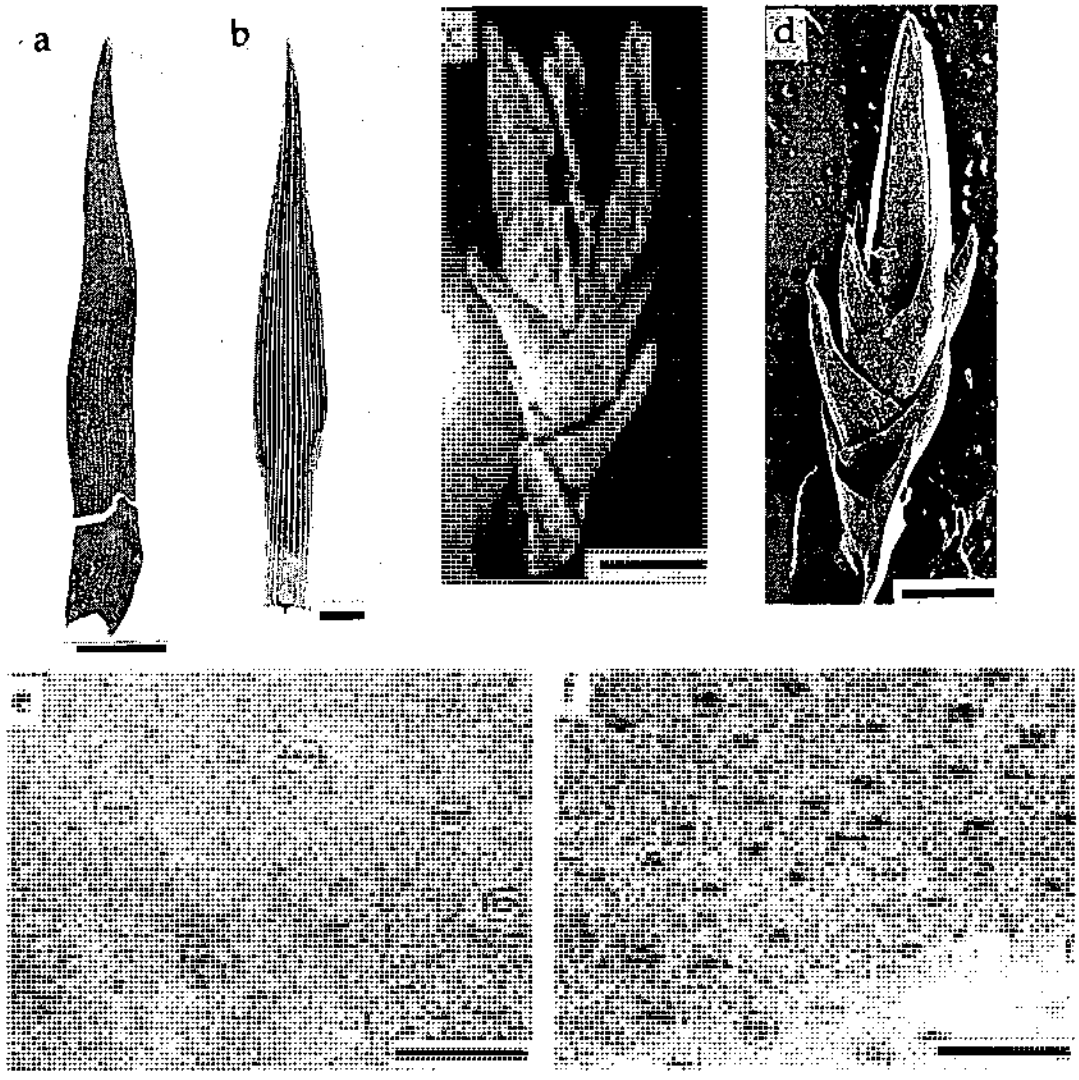


Figure 3.25 : *Richea/Dracophyllum* and *Sprengelia*. a : Fossil aff. *Richea milliganii / R. acerosa* leaf. Note the parallel venation and clasping leaf base. b : Extant *R. milliganii* leaf. c & e : Fossil *Sprengelia incarnata* from Melaleuca. d & f : Extant *S. incarnata*. c & d : Inflorescences with leaves. e & f : Cuticle. Note the extremely sinuous cells walls. Scale bars for a & b = 2 mm, for c & d = 1 mm, for e & f = 0.5 mm.

sedgeland-heath from lowland to alpine areas. *Richea sprengelioides* has similar foliage but the inflorescences are nearly globular. The fossil form is consistent in leaf size except with alpine forms.

Tribe Styphelidae

aff. *Cyathodes juniperina* (RE, RPU1&2)

Specimens examined : RE 8206-8249
RPU 389, 415, 476, 1031-1035

Discussion : These fossils (Figures 3.26 a & c) are consistent in all characters with *C. juniperina* (Figures 3.26 b & d). The fossils have the stomatiferous surface of the leaf with longitudinal bands of distinctive short trichomes obscuring the stomata (Figure 3.26 c), and hence are clearly members of the subfamily Styphelidae. The pungent lanceolate leaves are consistent with *C. juniperina* and differ in size and/or shape from other extant epacrid species. *Cyathodes juniperina* is a widespread and common understorey shrub in woodlands and forests of wetter parts of Tasmania from lowland to subalpine areas, although it is only common in lowland rainforest in western and south-western Tasmania.

aff. *Monotoca glauca* (ME & RE)

Specimens examined : ME 497-501
RE 8201-8205

Discussion : Jordan *et al.* (1991) illustrate this taxon. These seeds (Figure 3.26 e) are of a shape characteristic of *M. glauca* (Figure 3.26 f), which is now widespread and common in scrub and wet sclerophyll forest from lowland to subalpine areas in western Tasmania. The seeds of *Cyathodes* and other drupaceous epacrid genera are relatively broader than those of *Monotoca*. Other species of *Monotoca* differ in seed size.

***Trochocarpa* sp. (RE, RPU1&2)**

Specimens examined : RE 8250-8288
RPU 385, 428, 429, 495, 1093

Discussion : These ovate leaves (Figures 3.27 a & b) have five parallel veins apparent on the stomatal surface and have cuticle with highly

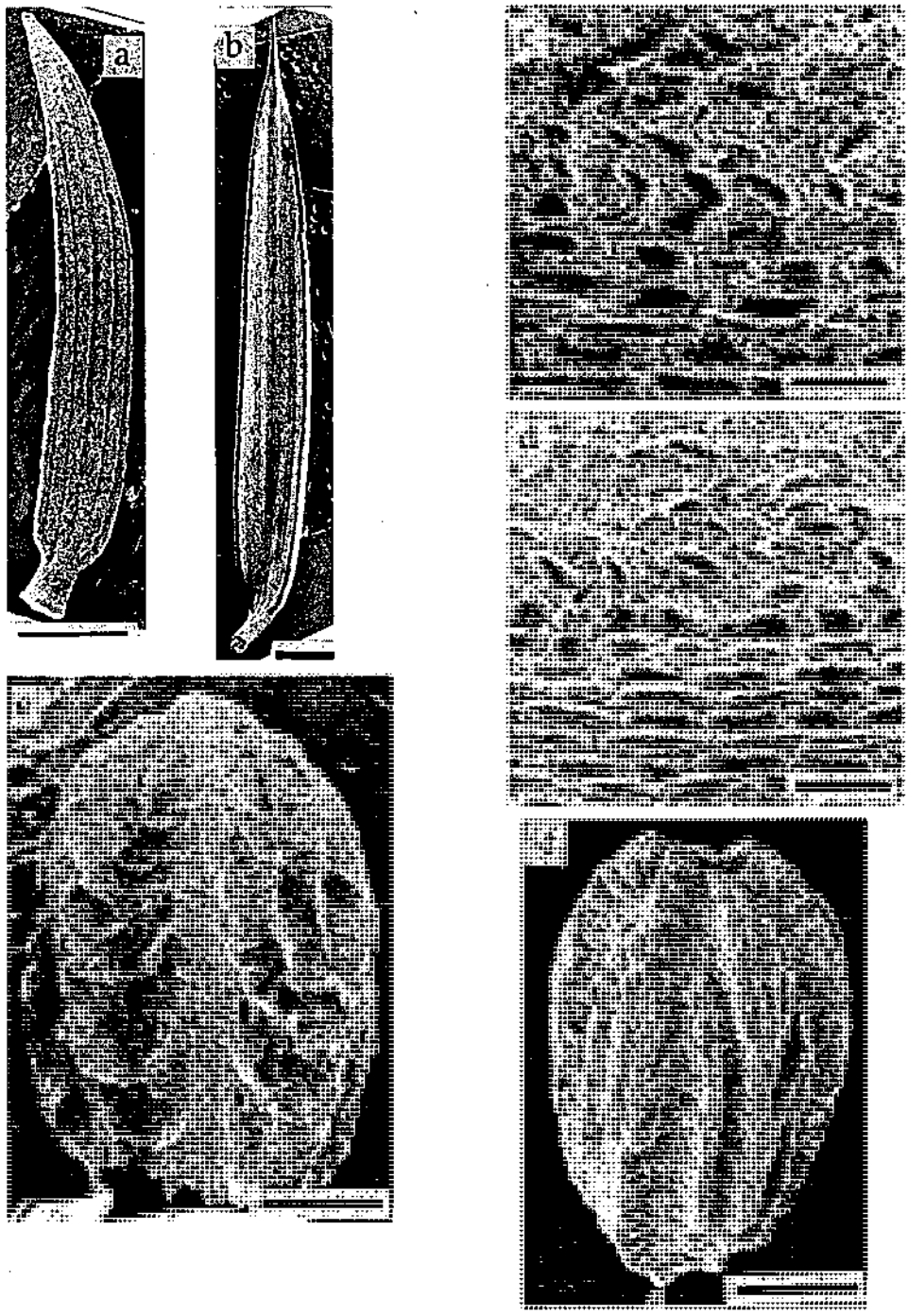


Figure 3.26 : Epacridaceae (cont.). a & c : Fossil aff. *Cyathodes juniperina* from Regatta Point. b & d : Extant *C. juniperina*. a & b : Leaves. c & d : Details of leaf surface showing characteristic trichomes obscuring stomata (arrows). e : Fossil aff. *Monotoca glauca* seed. f : Extant *Monotoca glauca* seed. Scale bars for a, b, e & f = 1 mm, for c & d = 50 µm.

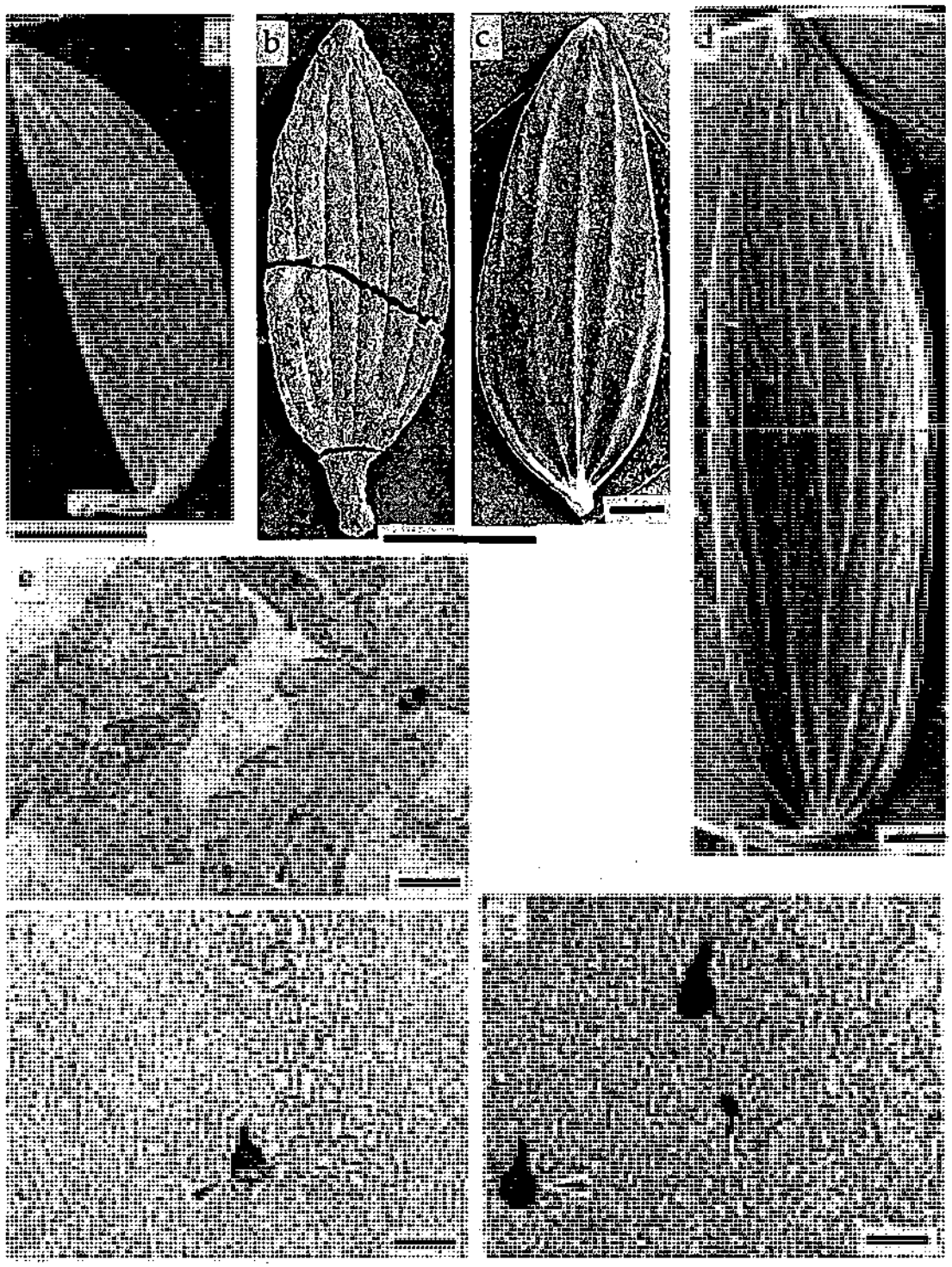


Figure 3.27 : *Trochocarpa*. a, b & e : Fossil *Trochocarpa* sp. from Regatta Point. c & g : Extant *T. cunninghamii*. d & f : Extant *T. gunnii*. a, b, c & d : Leaves. Note the twisted petioles in *T. gunnii* and one fossil and the straight petiole in *T. cunninghamii* and the other fossil. e, f & g : Cuticles. Note the sinuous cell walls, and trichomes (arrows). Scale bars for a, b, c & d = 10 mm, for e, f & g = 50 µm.

sinuous cell walls on both the stomatiferous surface and the non-stomatiferous surface, with characteristic trichomes (Figure 3.27 e) and aligned stomata which clearly indicate that this fossil taxon belongs to *Trochocarpa*. The fossils are similar to two extant Tasmanian species, *T. cunninghamii* and *T. gunnii* (Figures 3.27 c, d, f & g). The fossils differ in leaf size and shape from all other species of *Trochocarpa*. Some of the fossils (Figure 3.27 a) have twisted petioles, which are usual in *T. gunnii* (Figure 3.27 d). Others have straight petioles which are usual in *T. cunninghamii*. These fossils may therefore be from either or both of these extant species, or from one or more similar extinct *Trochocarpa* species. *Trochocarpa cunninghamii* and *T. gunnii* are understorey shrubs of rainforest of western Tasmania.

(?)Escalloniaceae

The Escalloniaceae are only known as macrofossils from the record of *Quintinia* cuticle from Regatta Point Upper by Hill and Macphail (1985).

? *Anopterus* (RPU1)

Specimen examined : RPU 318

Description : Leaf base narrowly cuneate. Venation brochidodromous below, semicraspedodromous above, secondary veins looping well within the margins, tertiary veins sparsely percurrent. Margin serrate apart from entire base. Teeth obtuse, convex on the basal side, convex on apical side. Outer surface of cuticles amorphous. Cuticle of stomatiferous surface with randomly oriented, unevenly paracytic stomata, prominent cuticular flange surrounding the guard cells on inner cuticular surface. Cuticle of non-stomatiferous surface showing ± hexagonal, isodiametric epidermal cells.

Discussion : This fossil (Figure 3.28 a) is clearly distinct in leaf form from any extant species in Tasmania. It is morphologically consistent with the Escalloniaceae and in particular with *Anopterus*. The two extant species of *Anopterus*, *A. glandulosus* and *A. macleayanus* differ vegetatively primarily in that *A. macleayanus* has hairy leaves which are larger than those of *A. glandulosus*. The attenuate base, entire basally and serrate above, with teeth pointed apically, concave on the apical side and convex

on the basal side are all characteristic of *Anopterus* (Figure 3.28 b). The stomatal morphology (Figure 3.28 c & e) with two uneven subsidiary cells, and a cuticular flange surrounding the guard cells is particularly characteristic of both species of *Anopterus* (Figures 3.28 d & f). The homology of these structures between the fossil and extant *Anopterus* is ambiguous. Other Escalloniaceae have rings of subsidiary cells around the stomates.

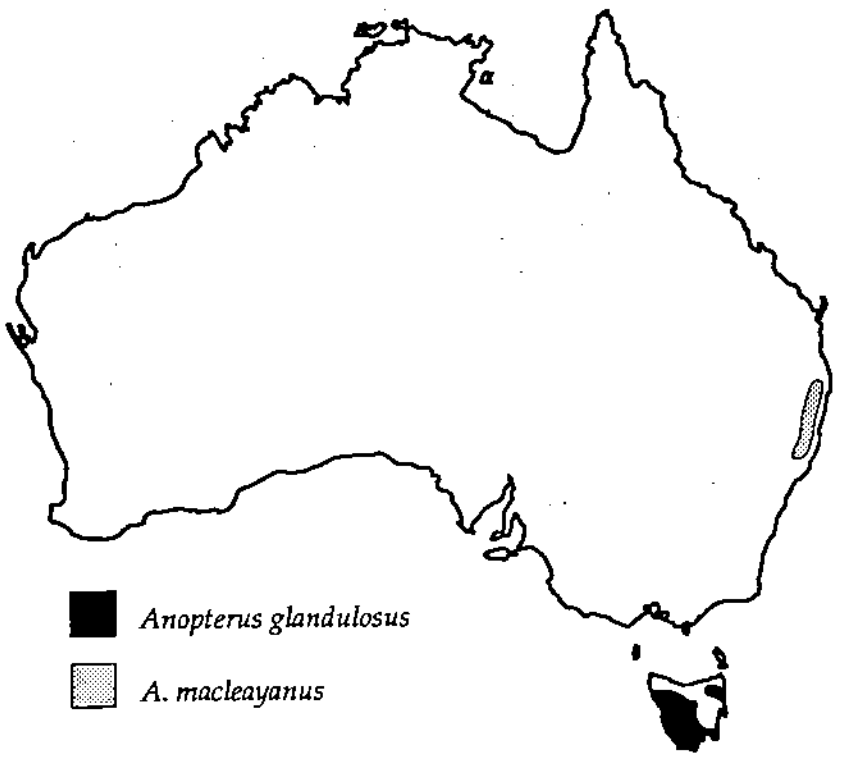


Figure 3.29 : Distribution of extant species of *Anopterus*.

There are a number of other groups with toothed leaves, semicraspedodromous venation and uneven paired subsidiary cells, especially in the Cunoniaceae (Hufford and Dickison 1992). None of the Cunoniaceae, share the combination of venation, stomatal form and entire base with toothed upper leaf. The fossil differs in several significant ways from *Anopterus*. The leaf base is less attenuate than extant *Anopterus*, the secondary veins of extant *Anopterus* species run parallel and close to the margins for much of their length (Figure 3.28 b), whereas the fossil's secondary veins loop distantly from the margin, and upper and lower

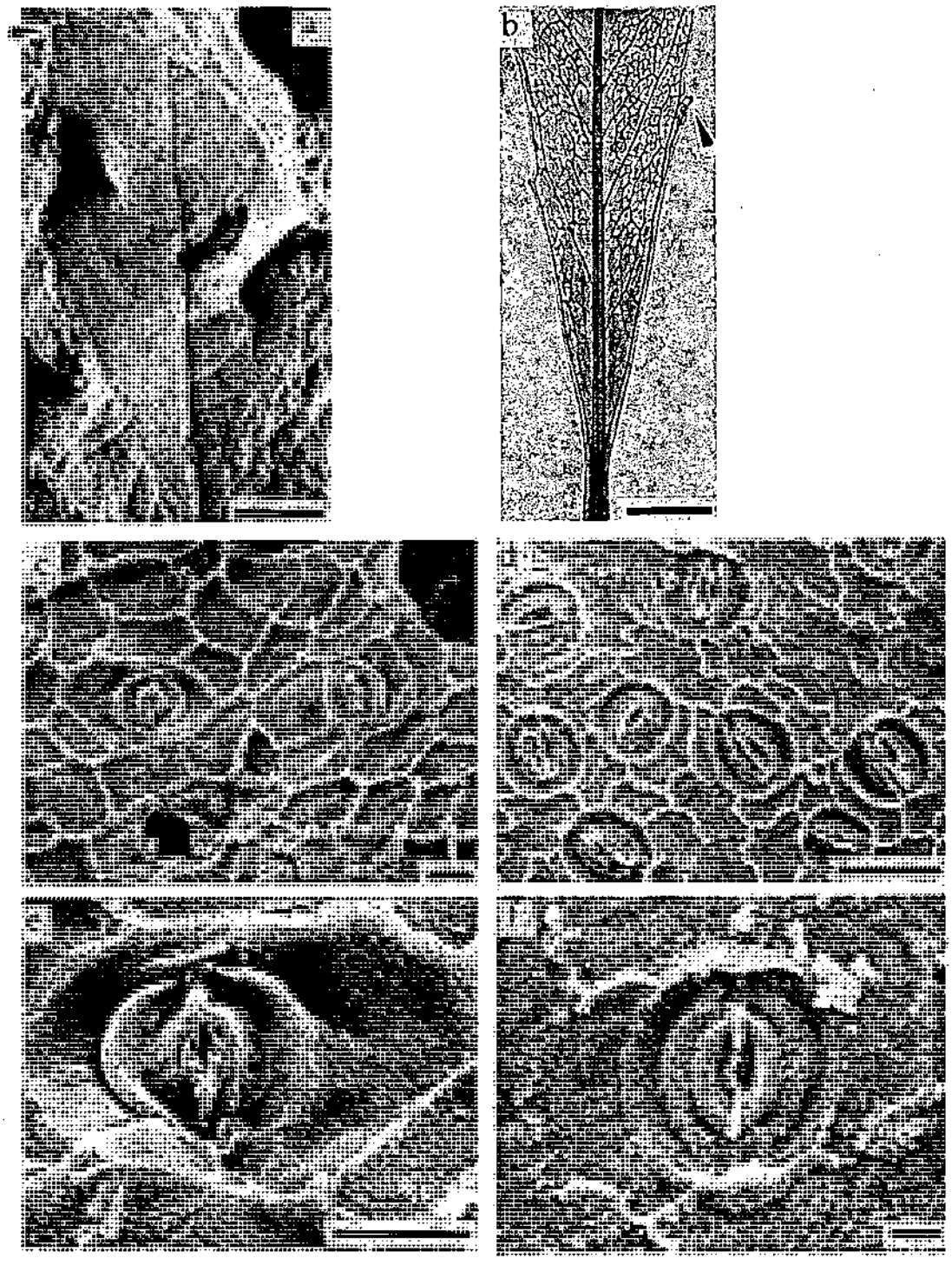


Figure 3.28 : *Anopterus*. a, c & e : Fossil ? *Anopterus* species from Regatta Point. b, d & f : Extant *Anopterus glandulosus*. a & b : Leaves. Note the entire leaf bases, the teeth (arrows) and the brochidodromous venation. c & d : Inner surfaces of cuticle of stomatiferous surface. e & f : Inner surfaces of the cuticle of the stomatiferous surfaces showing stomates. Scale bars for a & b = 10 mm, for c, e & f = 10 µm, for d = 50 µm.

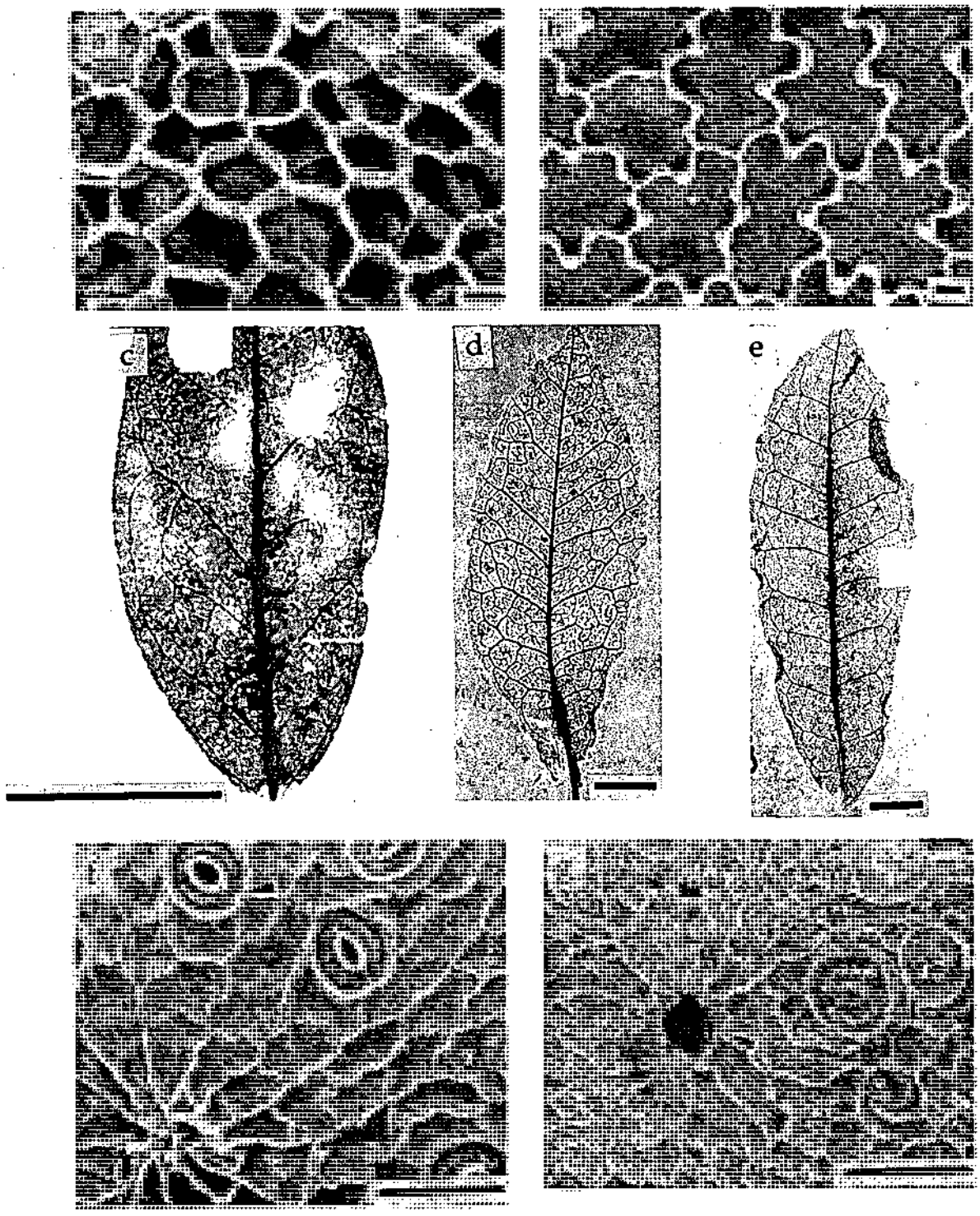


Figure 3.30 : Escalloniaceae. a & b : Inner surfaces of the cuticle of the non-stomatiferous surface. a : Fossil ? *Anopterus* from Regatta Point. b : Extant *A. glandulosus*. Note the sinuous cell walls. c, d, e, f & g : *Quintinia*. c & g: Fossil *Quintinia* sp. nov. from Regatta Point. d & f : Extant *Q. acutifolia*. e : *Q. sieberi*. c, d & e : Leaves. Note the looped secondary veins, and margin shapes. f & g : Inner surface of cuticle of stomatiferous surface. Note the heavy striations, circular stomata with T-pieces of cuticle at the stomatal poles (arrows) and the glands (arrows). Scale bars for a & b = 10 µm, for c, d & e = 10 mm, for f & g = 50 µm.

epidermal cells of extant *Anopterus* have sinuous anticlinal epidermal cell walls (Figures 3.30 b) whereas the fossil has upper and lower epidermal cells with straight anticlinal walls (Figures 3.30 a). This fossil is from a species which is certainly extinct in Tasmania and may be an extinct species of the genus *Anopterus*, which is extant in Tasmania.

The extant *Anopterus* species are understorey shrubs of temperate rainforest. *Anopterus glandulosus* is endemic to Tasmania and *A. macleayanus* occurs at high altitudes in northern New South Wales and southern Queensland (Figure 3.29). *Anopterus* species have large winged seeds (up to 2 cm long) borne in capsules (Stanley and Ross 1988), and are likely to be rather poorly dispersed.

Escalloniaceae

***Quintinia* sp. nov. (RPU1&2)**

Specimens examined : RPU 191, 345, 347, 384, 420, 443, 453, 505, 515, 518, 538, 556, 1094-1132

Diagnosis : Leaf entire, about 3 cm long. Cuticle with amorphous non staining outer layer. Inner layer of cuticle striate inside and out, stomata with broadly reniform guard cells and T-pieces of cuticle at the stomatal poles.

Type Specimen : RPU 556

Description : Leaf ovate, entire, about 3 cm long, about 1.2 cm broad, apex abruptly obtusely acuminate, margin irregular plane. Venation brochidodromous, mibrib prominent , secondary veins strong, third and fourth order venation randomly reticulate. Cuticle with an amorphous, non-staining outer layer, inner layer striate on inner and outer surfaces, with abundant, large, prominent, apparently deciduous glands. Cuticle of stomatiferous surface and radially striate around glands, concentrically striate around stomata, stomata with broadly reniform guard cells and T-pieces of cuticle at the stomatal poles.

Discussion : This taxon was identified as *Quintinia* from cuticle fragments and illustrated by Hill and Macphail (1985). These fossils (Figure 3.30 c) have leaf shape and venation consistent with *Quintinia* (Figure 3.30 d & e). The combination of the large glands and cuticle striate on both inner and outer surface are sufficient to identify this as *Quintinia*. Striate cuticles

are relatively widespread, occurring in groups such as Proteaceae, Rosaceae and Symplocaceae, but none of these taxa have cuticles which are striate on both inner and outer surfaces. The glands and stomata are also distinctive.

The cuticle morphology of the fossil (Figure 3.30 f & 3.32 a) shares characters with *Q. acutifolia* from New Zealand (Figure 3.30 g & 3.32 b) : semicircular guard cells, abundant deciduous glands and strong striations. The cuticles of both the fossil and *Q. acutifolia* appear to be composed of two layers, an amorphous, nonstaining thick outer layer and an inner layer which resemble ordinary cuticle. These characters are apparently derived since they do not occur in any close relatives of *Quintinia* and hence strongly suggest close phylogenetic relationship of the two species. *Quintinia sieberi* (Figures 3.32 c) from eastern Australia has glands and striate cuticle, but these are much less well developed than the fossil, and it does not have semicircular guard cells. Other species of *Quintinia* have fewer of these characters. Leaf margins tend to be variable within the genus, but most species have at least slightly irregular margins. The New Zealand species including *Q. acutifolia* have toothed margins. The Australian species have virtually entire margins, but Figure 3.32 c illustrates an extreme form of *Q. sieberi* with teeth. Entire margin appears to be a derived character, since other genera of the Escalloniaceae have teeth. The fossils are entire margined, so there is a conflict between the evidence of a sister relationship between the fossil and *Q. acutifolia* from the cuticle evidence, and evidence of a sister relationship with the Australian species on leaf architecture. The variability of leaf margins within species, however, suggests that the cuticle characters may be reliable. Hence it is likely that the fossils are closely related to *Q. acutifolia*, possible less closely related to *Q. sieberi* and more distantly related to other *Quintinia* species. The fossils bear little similarity to any of the Malesian species of *Quintinia* studied. These fossils are therefore from a species which is extinct from Australia and almost certainly globally, and from a genus which is extant in Australia and New Zealand but not Tasmania.

Quintinia species are mainly rainforest trees and shrubs of tropical and subtropical areas of Australasia and Malesia (Figure 3.31). *Quintinia acutifolia*

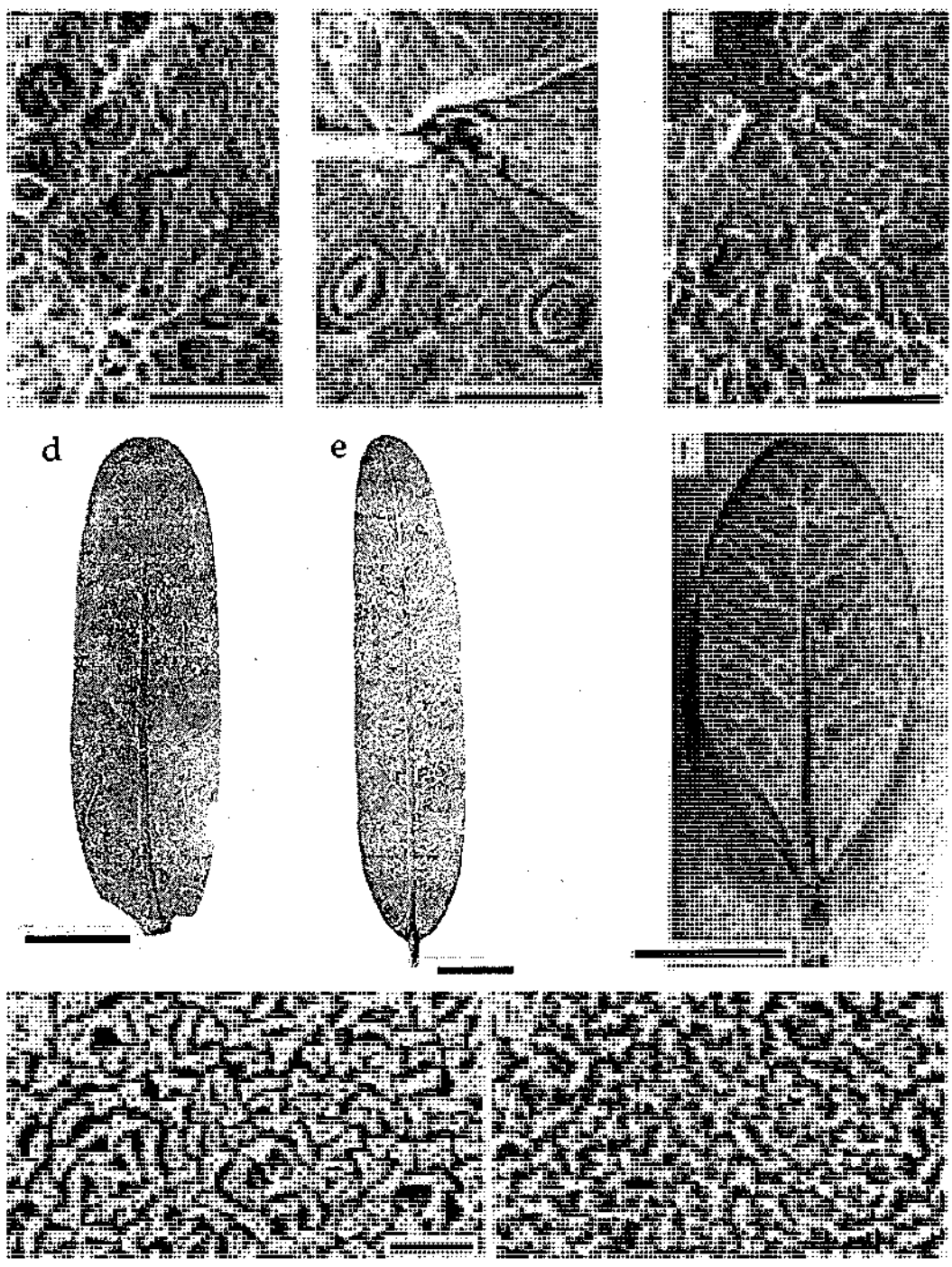


Figure 3. 32 : *Quintinia* and *Eucryphia*. a : Outer surface of stomatiferous surface of *Quintinia* sp. nov. from Regatta Point. Note the heavy striations. b : Outer surface of stomatiferous surface of *Q. acutifolia*. c : Inner surface of cuticle of stomatiferous surface of *Q. sieberi*. Note the less striate cuticle than the fossil, and lack of T-pieces. d, e, f, g & h : *Eucryphia*. d & g : Fossil *Eucryphia* from Regatta Point. d : Leaf. g : Outer surface of stomatiferous surface of leaf. Note the peltate trichomes covering the surface. e & h : Extant *E. lucida*. e : Leaf. h : Outer surface of stomatiferous surface of leaf. f : Extant leaf of *E. milliganii*. Scale bars for a, b, c, g & h = 50 mm, for d, e & f = 5 mm.

and other New Zealand species are primarily temperate rainforest shrub species. *Quintinia sieberi* is a rainforest tree or shrub from eastern Australia. *Quintinia* species have capsules with tiny spindle shaped seeds (Stanley and Ross 1983), and are likely to be poorly wind dispersed.

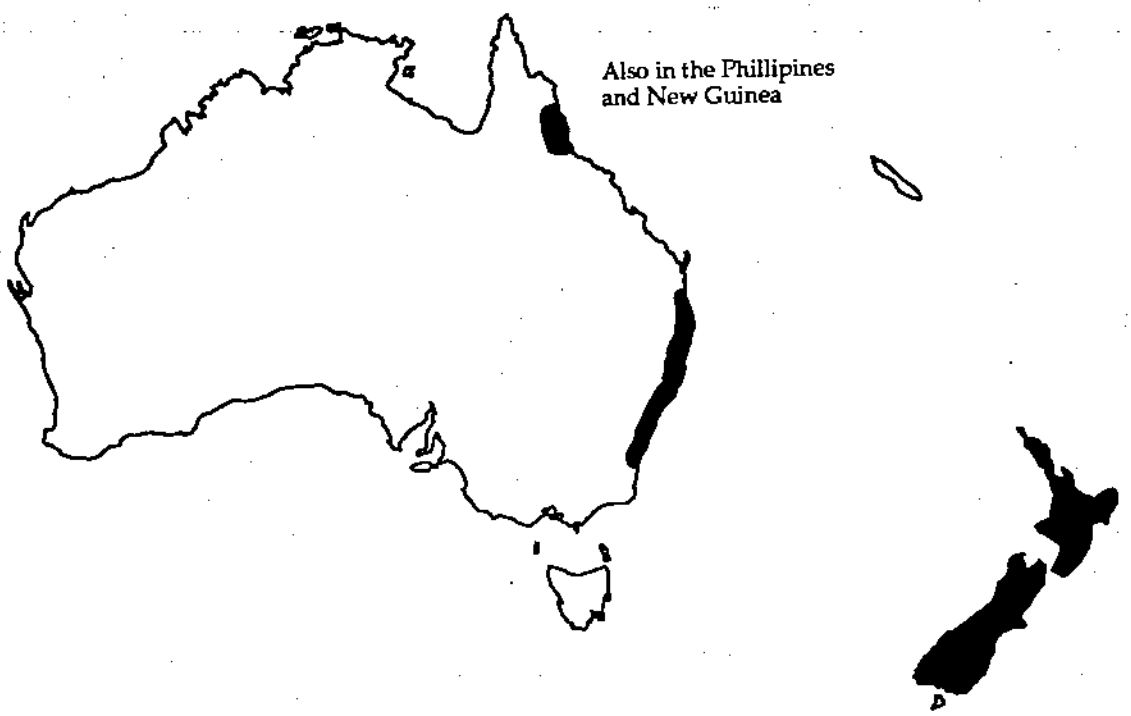


Figure 3.31 : Extant distribution of *Quintinia* species.

Eucryphiaceae

***Eucryphia* sp. (RPU1&2, ME)**

Specimens examined : ME 515
RPU 004-006, 085-090, 247, 348, 371, 373, 382, 411, 448, 475, 478, 546, 1133-1422

Discussion : Hill (1991 a, Hill and Macphail 1985) has assigned the fossil leaves from Regatta Point to *Eucryphia* on the basis of the occurrence of distinctive and diagnostic peltate trichomes on the stomatiferous surface (Figures 3.32 g), and illustrated them. The leaves of these fossils (Figure 3.32 d) are similar in shape and most features of cuticle morphology to *E. lucida* (Figure 3.32 e & h), *E. milliganii* (Figure 3.32 f) and leaflets of *E.*

moorei . The leaves cannot be readily assigned to *E. lucida*, *E. moorei* or *E. milliganii.* They differ from *E. lucida* in having non-peltate trichome bases extending up the midrib on the stomatiferous surface. They have fewer non-peltate trichome bases than is normal for either *E. moorei* or *E. milliganii* and the leaves are larger than is usual for *E. milliganii. Eucryphia* leaves have been found in several Tertiary Tasmanian deposits and are common Quaternary macrofossils in Tasmania (Hill 1991 a).

The Melaleuca fossil cannot be identified to species level since they are represented by dispersed cuticle fragments lacking sufficient diagnostic features.

Extant species of *Eucryphia* are rainforest trees or shrubs. The genus occurs in Australia and New Zealand. Two species occur in Tasmania : the lowland canopy tree *E. lucida*, and *E. milliganii* which is a tree or shrub of moderate to high altitudes. *E. moorei* is the dominant tree in some cool temperate rainforests of New South Wales, and an unnamed species is a shrub on some rocky areas at about 1200 m altitude on the very wet Mt. Bartle Frere in North Queensland. Two species, *E. cordifolia* and *E. glutinosa*, occur in very wet cool temperate rainforests of South America (Hill 1991 a). *Eucryphia* species have small winged seeds borne in capsules (Curtis and Morris 1975) and are likely to be poorly wind dispersed.

***Eucryphia lucida* (RE) and *E. milliganii* (RE)**

Specimens examined : RE 6710-7059 (*E. lucida*)
RE 7060-7547 (*E. milliganii*)

Discussion : Fitzsimons *et al.* (1990) distinguished between these fossil species on the basis of leaf size. Reassessment of the fossils based on the characters of Hill (1991a) confirms the presence of both species.

Fabaceae

***Oxyloblum* sp. nov. (RPU1&2)**

Specimens examined : RPU 489, 551, 573, 2420-2443

Diagnosis : Leaves cruciate with pungent lobes, apical lobe longer than lateral lobes. Venation reticulate apart from midrib and single

secondary veins leading to lateral lobes. Cuticle of stomatiferous surface without papillae, stomata not obscured by cutin lobes, two to four unevenly sized subsidiary cells.

Type Specimen : RPU 573

Description : Leaves cruciate, about 1.2 cm long, 1.5 cm broad. Strong primary vein leading to apex, a single equally strong secondary vein leading to each lateral lobe, elsewhere venation reticulate. Base attenuate, about 3 mm broad immediately basal of lateral lobes. Petiole less than 1 mm. Apical lobe about 2 mm long, reflexed, acute, pungent. Each lateral lobe about 2 mm wide at base, slightly tapered, obtuse with pungent mucro. Cuticle of stomatiferous surface with stomata restricted to lacunae between veins, stomata randomly oriented, subsidiary cells of unequal sizes, two or three per stomate, paler staining than other epidermal cells, partially formed stomata present. Cuticle of non-stomatiferous surface unknown.

Discussion : Cruciate leaves such as these fossils (Figure 3.33 a & b) occur in several groups including Fabaceae and Proteaceae. The combination of cruciate leaf shape, reticulate venation apparent on the cuticle of the stomatiferous surface and anomocytic stomata, however, almost certainly precludes any group except the Mirbelieae (Fabaceae) which includes, among others *Oxylobium*, *Gastrolobium*, *Nemcia*, *Mirbelia* and *Chorizema*. Some forms of *O. ilicifolium* from the Blue Mountains in New South Wales have been described as *O. staurophyllum*, although (Wiecek 1991) do not recognise this species. These forms (Figure 3.33 c) have leaves which are cruciate like the fossil, but most leaves usually have some degree of secondary lobing, which has not been observed in any of the many fossil leaves studied, and the apical lobe is longer than the lateral lobes, whereas the lateral lobes are considerably longer than the apical lobes in the fossil. Some other members of the Mirbelieae, all from south-western Australia, also have leaf shapes similar to the fossil, in particular *Mirbelia dilatata* (Figure 3.33 d) and *Gastrolobium spinosum* var. *trilobum*, but also *Nemcia triloba* (Figure 3.33 e) which has larger, less deeply lobed leaves. *Oxylobium* is likely to be polyphyletic and *O. ilicifolium* and its close relatives could possibly be incorporated into *Gastrolobium*, with *Nemcia* being closely related (Crisp and Westem 1987).

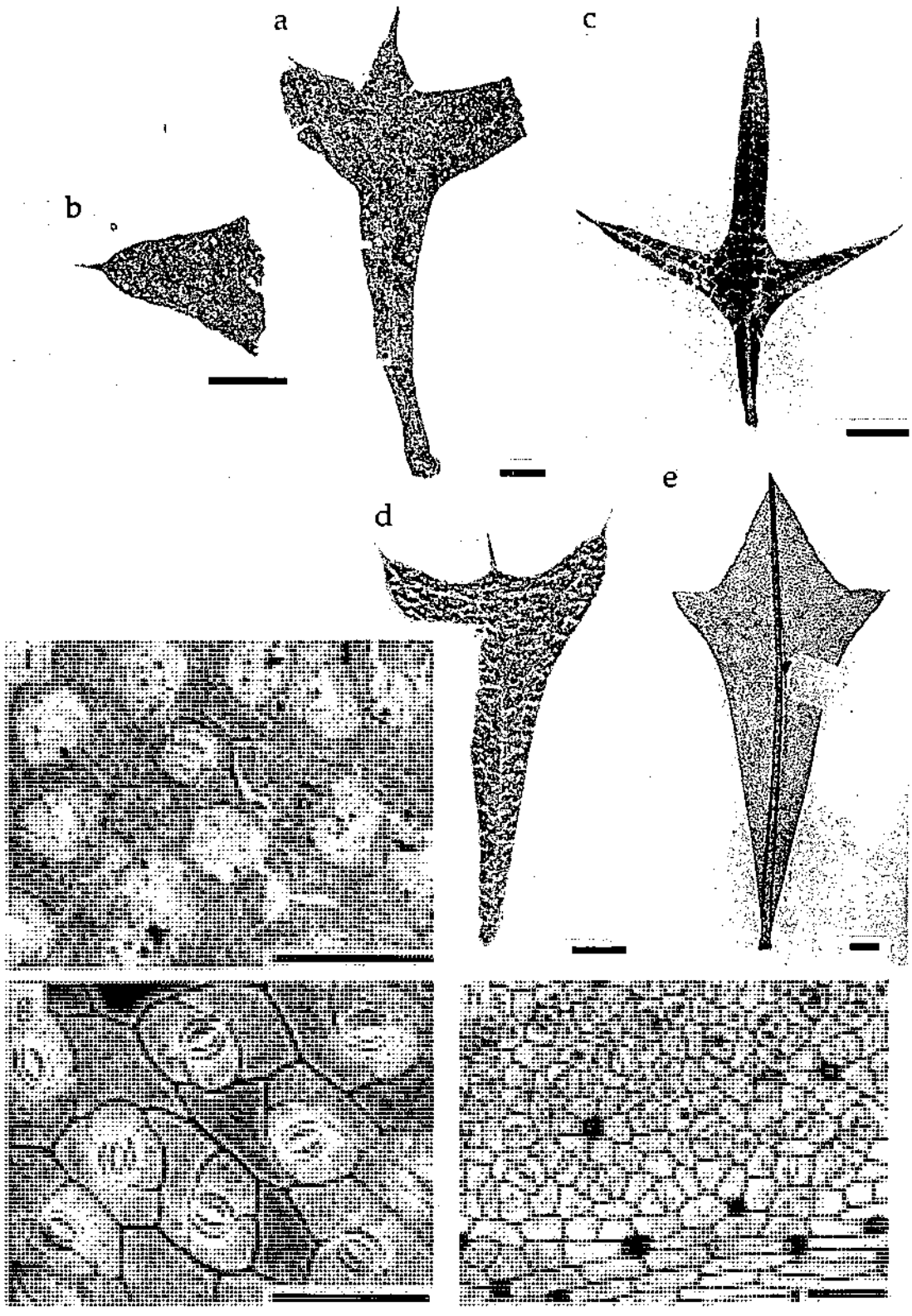


Figure 3.33 : Fabaceae. a, b & f : Fossil *Oxylobium* sp. nov. from Regatta Point. a : Leaf. b : Fragment of lateral leaf lobe. Note the obtuse mucronate apex. f : Cuticle of stomatiferous surface. c & g : Extant *O. ilicifolium* from the Blue Mountains, New South Wales ('*O. staurophyllum* ') (CBG 8501928). c : Leaf. g : Cuticle of stomatiferous surface. d & h : Extant *Mirbelia dilatata* (CBG 8700217). d : Leaf. h : Cuticle of stomatiferous surface. Note the trichomes, papillae and obscured guard cells. e : Leaf of extant *Nemcia triloba* (CBG 035586). Scale bars for a, b, c, d & e = 2 mm, for f, g & h = 100 µm.

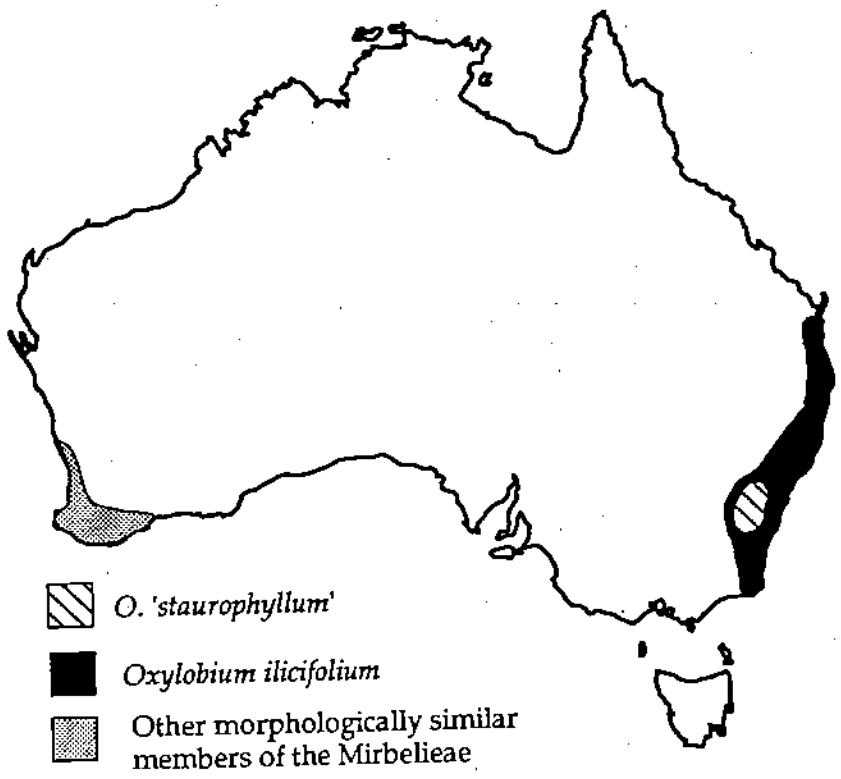


Figure 3.34 : Distribution of extant *Oxylobium ilicifolium*, including *O. staurophyllum*. The distribution of other morphologically similar species is also shown.

The cuticle of the stomatiferous surface of this fossil (Figure 3.33 f) is virtually indistinguishable from that of *O. ilicifolium* (Figure 3.33 g). The cuticle morphology of the fossils, however, appears to be ancestral within the *Oxylobium* group, since *Bossiaea* species and *Platylobium* species have cuticles which are similar, except that closely reticulate venation is not apparent on the cuticle of the stomatiferous surface. The cuticle similarities do not, therefore, necessarily indicate a close relationship of the fossil with *O. ilicifolium*. The cruciate leaf form is, however, almost certainly derived, and thus provides some evidence of close relationship of the fossil with *O. ilicifolium*. Members of *Mirbelia* (Figure 3.33 h), *Gastrolobium* and *Nemcia* have cuticular trichomes, small guard cells and subsidiary cells with single papillae and cutin lobes partly obscuring the guard cells, hence the fossil taxon is unlikely to be a member of any of these genera. Hence the fossils are from the Mirbelieae and are likely to be closely related to *O. ilicifolium*. They are tentatively assigned to *Oxylobium* until the taxonomic

inconsistencies within this group are resolved.

The Mirbelieae is widespread in Australia. The distribution of *O. ilicifolium* is shown in Figure 3.34. All the extant species morphologically similar to the fossil are highly sclerophyllous shrubs of heath or open forest on very nutrient poor soils. The fossils are also highly sclerophyllous. This is the only macrofossil record of the Fabaceae in Tasmania, except for a probable species of *Daviesia* from the Oligocene Cethana sediments (Carpenter 1991). I am aware of no reliable fossil record of the Fabaceae from Australian sediments. The fossils are from a species which is clearly extinct, but are likely to be closely related to a form of *O. ilicifolium* which grows on the depauperate siliceous soils of the Blue Mountains near Sydney.

Fagaceae

***Nothofagus cunningamii* (ME, RE, RPU1&2)**

Specimens examined : ME 516-520
RE 0001-4455
RPU 001-003, 009-013, 041-049, 052-059, 063-080, 095, 231, 234, 236, 241-246, 345, 359, 362, 375, 419, 449, 452, 458, 471, 484, 486, 487, 2444-4063

Discussion : The fossil record of *Nothofagus* in Tasmania, including this taxon, is described in Hill (1991 b). This fossil taxon was illustrated by Hill and Macphail (1985) and recorded by Fitzsimons *et al.* (1990) and Jordan *et al.* (1991).The fossil leaves and cupules from the Regency sediments are indistinguishable from extant *N. cunninghamii*, with several characters diagnostic of the species. The Melaleuca Inlet *Nothofagus* leaf fossils are poorly preserved but are consistent in leaf form and cuticle with *N. cunninghamii*. The RPU1 fossil leaves (Figure 3.35 a & c), cupules (Figure 3.36 a) and cuticles (Figure 3.35 d) all apparently fall into the extant range of *N. cunninghamii* (Figure 3.35 b & e, 3.36 b). However, the distribution of log transformed leaf lengths shows two nearly discrete, roughly normally distributed groups (Figures 5.4). The implications of this

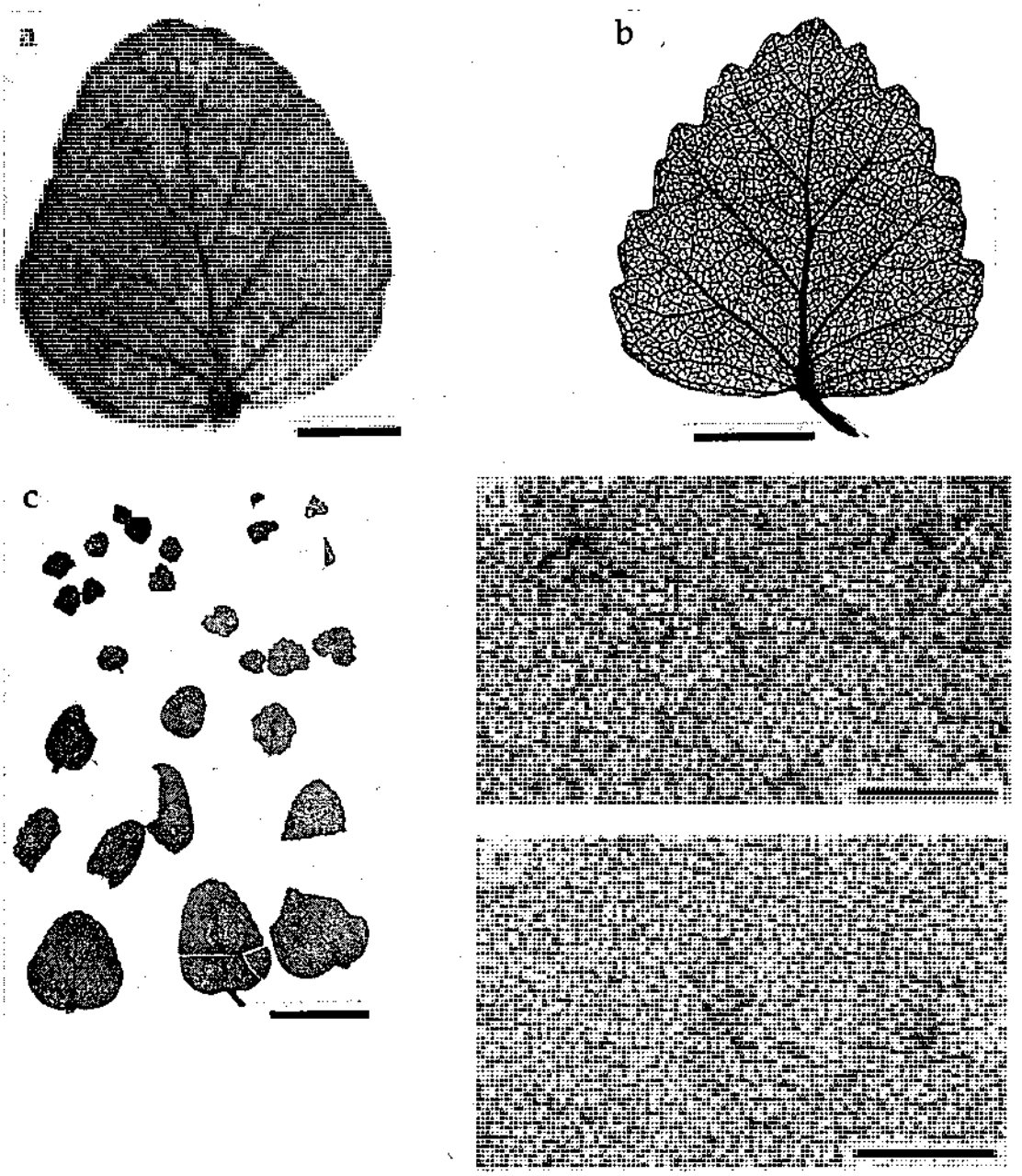


Figure 3.35 : *Nothofagus cunninghamii*. a, c & d : Fossil *N. cunninghamii* from Regatta Point. a : Leaf. c : Leaves from RPU1. Note the wide range of sizes d : Cuticle of stomatiferous surface. b & e : Extant *N. cunninghamii*. b : Leaf. e : Cuticle of stomatiferous surface. Scale bars for a & b = 0.5 mm, for c =2 mm, for d & e = 100 µm.

are discussed in chapters 5 and 6.

Nothofagus cunninghamii is usually a dominant of cool temperate rainforest of Tasmania and Victoria, but also occurs as a sub-alpine shrub. It is considered to be fairly poorly dispersed (Hickey 1982) and is capable of maintaining populations under low-moderate fire frequencies (Jackson 1968). The genus is widespread in cool temperate rainforest of Australia, New Zealand and South America, except for one sub-genus, *Brassospora*, which occurs in high altitude tropical rainforest in New Guinea and New Caledonia, although it extends to low altitudes (about 200 m a.s.l.) on very depauperate soils in New Caledonia. The seeds of the species of this subgenus are poorly dispersed, and have short viability (van Steenis 1972).

***Nothofagus* ? *gunnii* (RPU1)**

Specimens examined : RPU 419, 4594

Discussion : Cupules consistent in size and shape with *N. gunnii* and inconsistent with *N. cunninghamii* occur in the RPU1 sediments (Figure 3.36 c). The cupules are larger, the valves are broader, and the base is more massive than in extant *N. cunninghamii* (Figure 3.36 b), but are consistent in all these characters with *N. gunnii* (Figure 3.36 d). The most diagnostic cupule character separating subgenus *Fuscaspora*, which includes *N. gunnii*, from subgenus *Lophozonia*, which includes *N. cunninghamii*, is that the cupule lamellae are glandular in subgenus *Lophozonia*, and leaf-like in subgenus *Fuscaspora*(Hill and Read 1991). These lamellae have been eroded away on the fossil, and so it is not possible to clearly assign the fossils to subgenus *Fuscaspora*.

Nothofagus gunnii is a deciduous shrub or tree of alpine and subalpine rainforest and shrubberies of western and southern Tasmania. It is often found in association with *Athrotaxis* species, and is considered to be fire sensitive. Hill (1984) attributes a fossil leaf from the Oligocene sediments at Cethana in western Tasmania to *N. gunnii*. *Nothofagus gunnii* leaves also occur in Late Pleistocene sediments at Regatta Point in association with other now subalpine to alpine taxa including *Orites milliganii* and *O. revoluta* (G. J. Jordan unpublished).

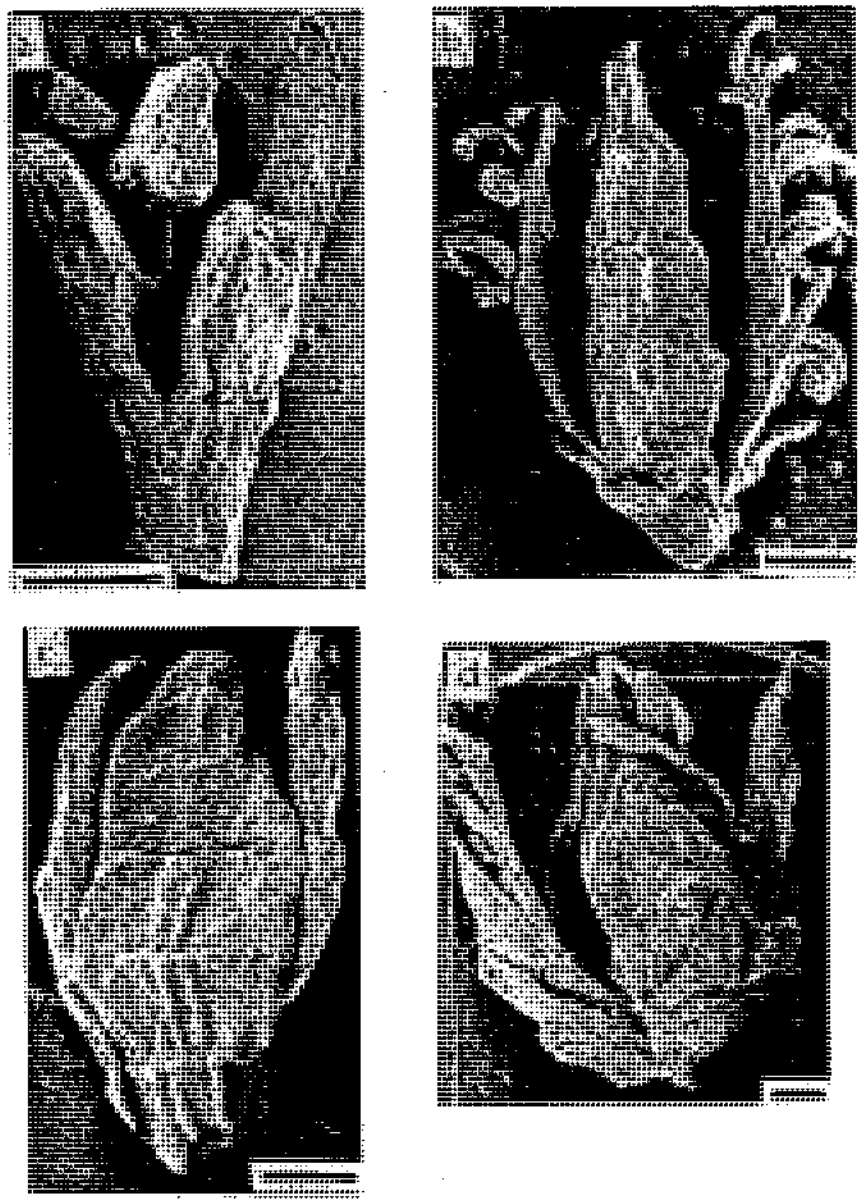


Figure 3.36 : *Nothofagus* cupules. a : Fossil *N. cunninghamii* from Regatta Point. The lamellae have been eroded away. b : Extant *N. cunninghamii*. The glandular lamellae have been stripped from one valve. c : Fossil *N.* ? *gunnii* from Regatta Point. Note the robust base and the broad valves unlike b and similar to d. d : Extant *N. gunnii*. Scale bars = 1 mm.

Laurophyllum sp. (RPU2)

Specimens examined : RPU 507, 512, 526-529, 535, 539, 544, 567, 4064-4095

Description : Leaves elliptic to ovate, about 3-5 cm long, about 1.2-2.0 cm broad. Apex obtusely acuminate, base slightly oblique. Petiole about 4 mm long. Margins revolute. Venation brochidodromous with about 7-8 pairs of secondary veins, tertiary venation weakly percurrent, higher order venation random reticulate, with no free ending veinlets. Cuticle of stomatiferous surface with stomata restricted to areoles between higher order veins. Stomata randomly oriented, guard cells small sunken more deeply than subsidiary cells, subsidiary cells paired, lateral, even, symmetric. Cuticle of non-stomatiferous surface with irregularly arranged isodiametric epidermal cells, trichome bases common.

Discussion : These leaves (Figure 3.37 a & b) are totally consistent in size, shape and venation with extant Lauraceae (Figure 3.37 c) except the subfamily Cassythae which are leafless parasites. There are, however, many other groups with broadly similar leaf shape and venation. The cuticle (Figures 3.37 d & f) is strongly suggestive of Lauraceae (Figure 3.37 e). The tiny guard cells sunken deeply below the subsidiary cells together with the presence of a cuticular scale associated with the subsidiary cell (Figures 3.37 e) are considered to indicate the family Lauraceae (Hill 1986). The leaves are therefore likely to be lauraceous. Within the Lauraceae identification of taxa using only leaves is more difficult. Hill (1986) argues that genera of Lauraceae can rarely be distinguished reliably on the basis of leaves and uses the form genus *Laurophyllum*.

The Lauraceae excluding *Cassytha* is widespread in rainforest and wet forests of the tropics and subtropics, and in Australia extends to southern New South Wales (see Figure 3.38). Lauraceous fruits are often dispersed efficiently by birds eating the fruit and defecating the seeds elsewhere (e.g. Howe 1986). There is an extensive Tertiary macrofossil record of the Lauraceae from Australia (Duigan 1950; Hill 1986). Many undescribed lauraceous leaf fossils occur in Tasmanian Early Tertiary sediments (R. S. Hill pers. comm.). The fossils differ in leaf architecture from any plant species extant in Tasmania, and in cuticle morphology from any plant

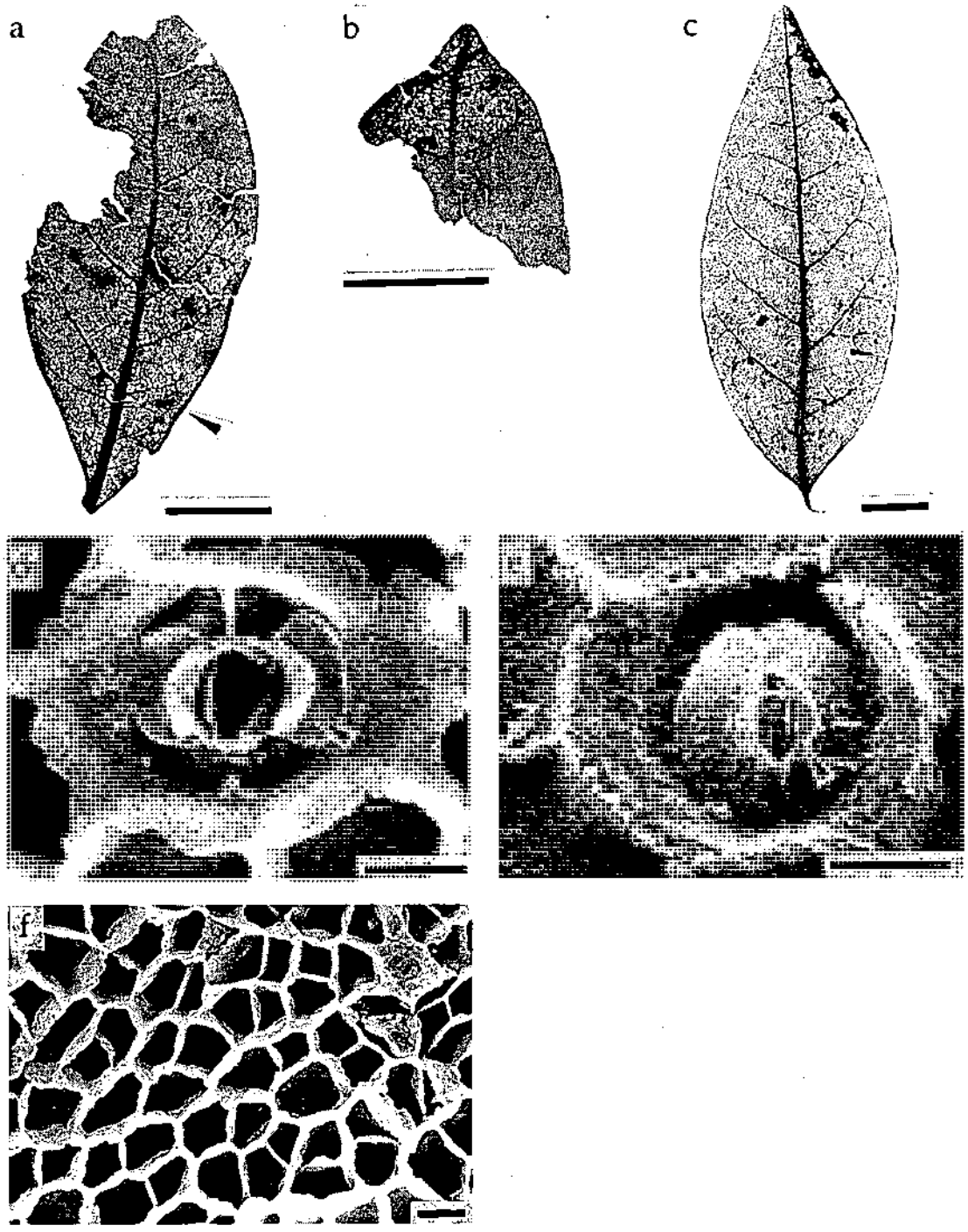


Figure 3.37 : Lauraceae. a, b, d & f : Fossil *Laurophyllum* sp. from Regatta Point. c : Cleared leaf of extant *Cryptocarya novae-anglica*. e : Extant *Cryptocarya* sp. nov. from the Bellenden Ker Range. a & b : Partial leaves. Note the drip tip and the slightly thickened margin (arrow). d & e : Inner surfaces of cuticle of stomatiferous surface, showing stomates. Note the small raised guard cell (arrows) and the cuticle lip within the aperture formed by the large subsidiary cells. f : Inner surface of non-stomatiferous surface. Scale bars for a, b & c = 10 mm, for d, e & f = 10 μm.

studied. They are therefore extinct from Tasmania, and are very likely to be members of the Lauraceae which is extinct from Tasmania except for the leafless parasite *Cassytha*.

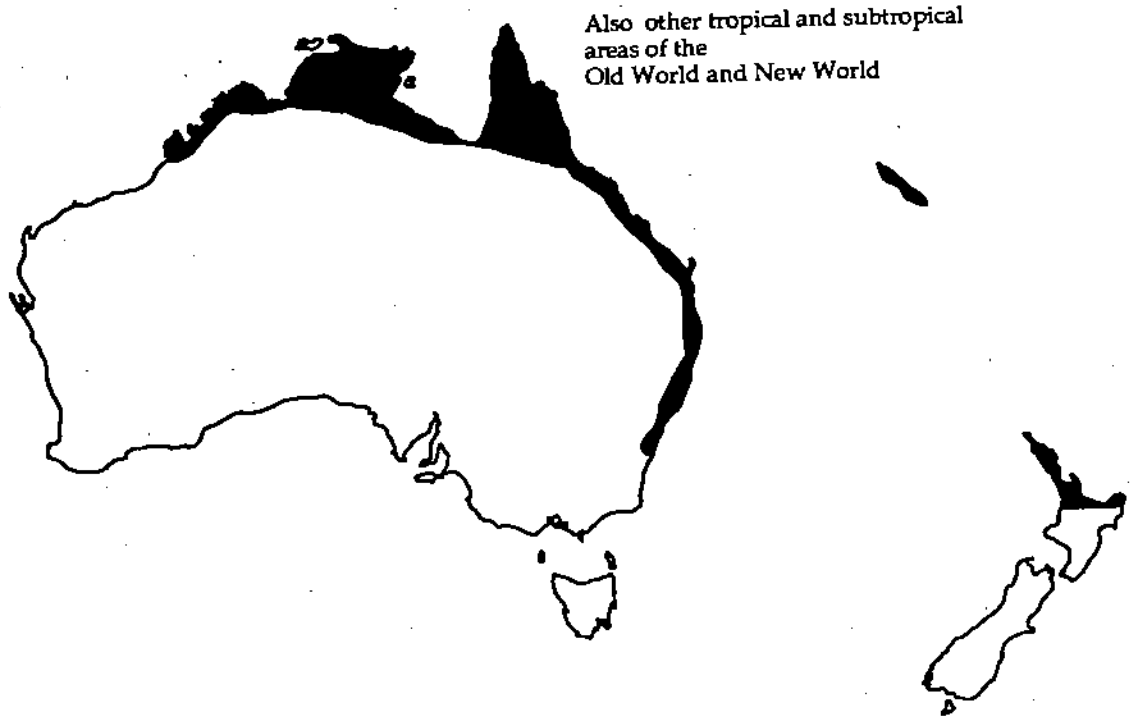


Figure 3.38 : Extant distribution of broad leaved Lauraceae.

Mimosaceae

Acacia

Phyllodinous *Acacia* species are widespread in Australia and occur occasionally elsewhere in the world (e.g. *A. koaia* in Hawaii). *Acacia* species with broad phyllodes live in a very wide range of habitats in Australia, from disturbed rainforests from the tropics to cool temperate areas, and to the arid zone, but not from alpine areas. The seeds are generally hard and relatively heavy, and therefore are usually poorly dispersed. They are, however, very long lived and resistant (Farrell and Ashton 1978; New 1984), and occasional long distance dispersal events (e.g. by water, or birds) may occur. The fossil record of *Acacia* is scanty. Cookson (1954) records the occurrence of pollen attributable to *Acacia* in Pliocene and Miocene sediments in Victoria, Australia and of a probable

phyllode from one of these sites : the Upper Pliocene Grange Burn site. She discounts earlier records as unreliable. *Acacia* pollen also occurs in Tasmanian Tertiary and Quaternary sediments.

***Acacia melanoxylon* (RPU2)**

Specimens examined : RPU 517, 4098-4337

Discussion : This fossil taxon (Figures 3.39 a) falls within the morphological range of extant *A. melanoxylon* (Figure 3.39 b), although the venation is unusual for *A. melanoxylon* in that the two or three major veins are scarcely more prominent than minor longitudinal veins which tend to be less oblique and anastomosing than most forms of *A. melanoxylon.* The cuticle of the fossil (Figures 3.39 c), although fragmentary, is consistent with *A. melanoxylon* (Figure 3.39 d). Similar cuticle occurs in a number of other *Acacia* species, but not in any with similar leaf size and venation in the wide ranging collections at the University of Tasmania and HO.

Acacia melanoxylon is a tree species with extremely wide distribution and ecological range. It occurs in wet forests, mainly within 100 years or so of disturbance, from southern Tasmania to the Atherton Tableland in north Queensland. In Tasmania it also occurs in dry woodland and as a coastal shrub, and as the dominant tree of swamp forest. It appears to be dependant on disturbance.

***Acacia* ? *mucronata* (ME)**

Specimens examined : ME 521

Discussion : This fossil taxon was recorded and illustrated in Jordan *et al.* (1991). This fossil taxon is only known from dispersed cuticle (Figure 3.39 e) which is consistent with *A. mucronata* (Figure 3.39 f) and is distinct from other extant Tasmanian species. *Acacia mucronata* is widespread and abundant in scrub and sclerophyll forest in much of southern Australia.

***Acacia* sp. nov. (RPU1)**

Specimens examined : RPU 050, 222, 230, 316, 344, 382, 430-432, 441, 446, 447, 462,

Diagnosis : Phyllodes with occasionally anastomosing venation with 3-4 prominent longitudinal veins, one leading to a single thick, reniform

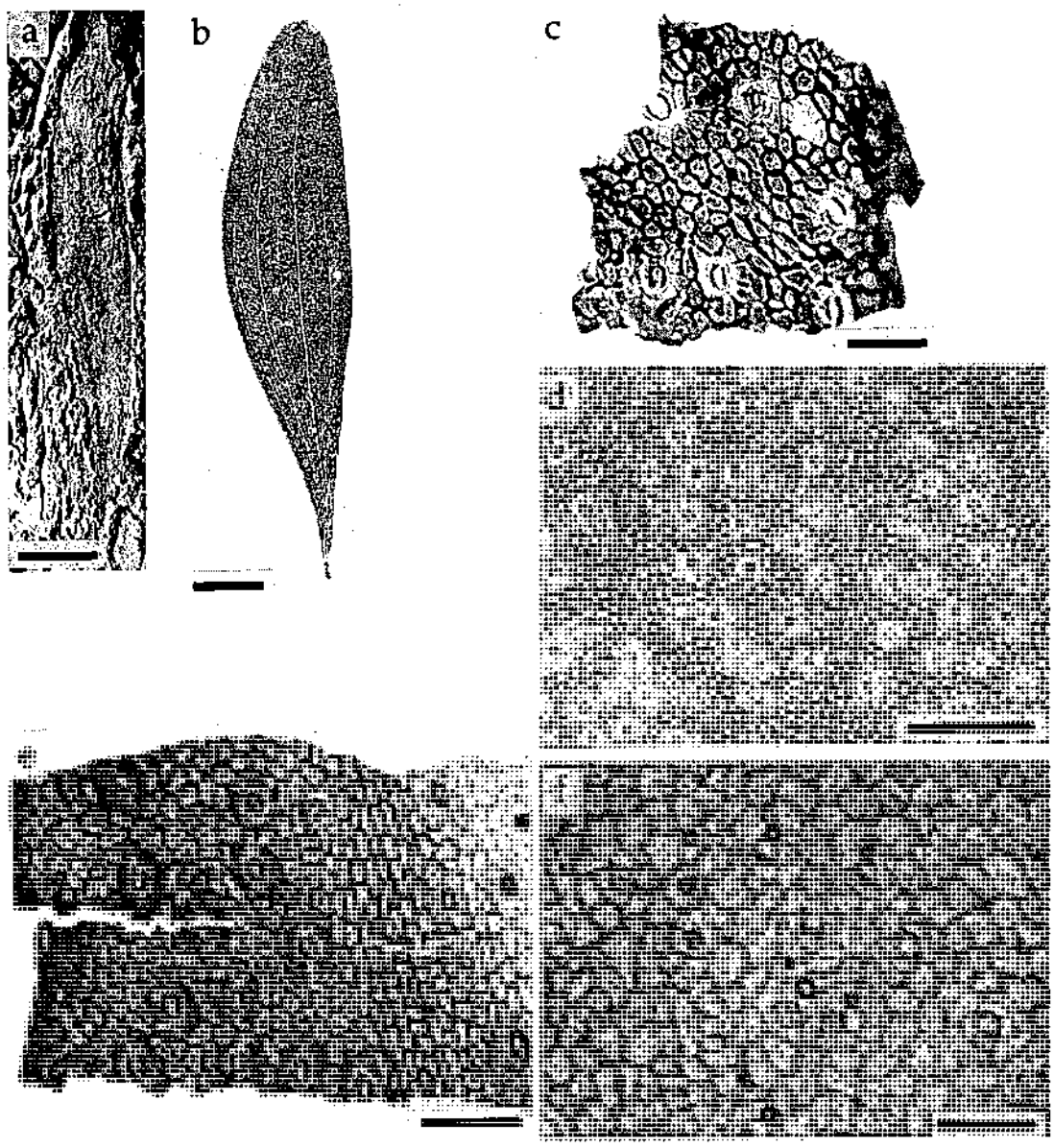


Figure 3.39 : *Acacia*. a & c : Fossil *Acacia melanoxylon* from Regatta Point. a : Phyllode. c : Cuticle. Note the circle of lighter staining subsidiary cells surrounding the small stomata. b & d : Extant *A. melanoxylon*. b : Phyllode. Note the reticulate venation and the lack of a conspicuous nectary. d : Cuticle. The subsidiary cells are circles of cells surrounding the small stomata. e : Cuticle of fossil *A.* ? *mucronata* from Melaleuca Inlet. Note the circle of darker staining subsidiary cells surrounding the stomata, which are larger than those of *A. melanoxylon*. f : Extant *A. mucronata*. Note the similar stomata to the fossil *A.* ? *mucronata*. Scale bars for a & b = 10 mm, for c = 50 μm, for d, e & f = 100 μm.

nectary about 1/4 along one margin, 3-4 mm long, about 1.5 mm wide. Stomata with 2-3, occasionally up to 5 subsidiary cells, stomatal axes mostly ± aligned with main axis of phyllode.

Type Specimen : RPU 316.

Description : Phyllodes oblanceolate, basal part ± curved up to the gland, 4 - (?)10 cm long, 1 - 2.5 cm broad, thick, apex obtuse, base slightly attenuate. Pulvinus about 2 - 3 mm long. A prominent, thick, reniform nectary about 1/4 way along one margin, 3 - 4 mm long, about 1.5 mm wide, orifice about 1 mm long centrally placed and facing outwards. Main veins apparently diverging from the base, one leading to the nectary, 2 - 4 extending up the phyllode. Longitudinal secondary veins about 10 - 15 per cm, often anastomosing. Stomata ± aligned with the long axis of the phyllode, 2 or 3 (- 5) subsidiary cells lateral to the guard cells.

Discussion : This fossil taxon was recorded by Hill and Macphail (1985) as an undetermined *Acacia* species. The slightly assymetrical form of these fossils (Figure 3.40 a, b & d) with uneven, parallel anastomosing veins, the presence of a prominent nectary along one margin and of a pulvinus, together with similar cuticle on both surfaces with stomata with somewhat irregular subsidiary cells combine to unequivocally identify these fossils as *Acacia* phyllodes. There are many species with phyllodes within this size range but none with such a prominent nectary located sub-basally. The list of comparable species with similar venation and leaf shape is rather short (i.e. *A. sophorae* and a few others). In particular, the fossils differ from the extant Tasmanian species *A. melanoxylon* (Figure 3.39 c) or *A. sophorae* (Figure 3.40 c) in significant ways :

(1) Both *A. sophorae* and *A. melanoxylon* have small basal nectaries,

(2)*Acacia melanoxylon* (Figure 3.39 d) has much smaller stomata which generally have about 6 lateral subsidiary cells with thin cuticle. *Acacia sophorae* (Figure 3.40 e) and the related *A. longifolia* have frequent and prominent glands apparent in the cuticle.

(3)*A. melanoxylon* has secondary veins with finer reticulation.

The fossil is therefore from a species which is extinct from Tasmania, and almost certainly globally extinct and from a genus and foliage form which is widespread in Australia.

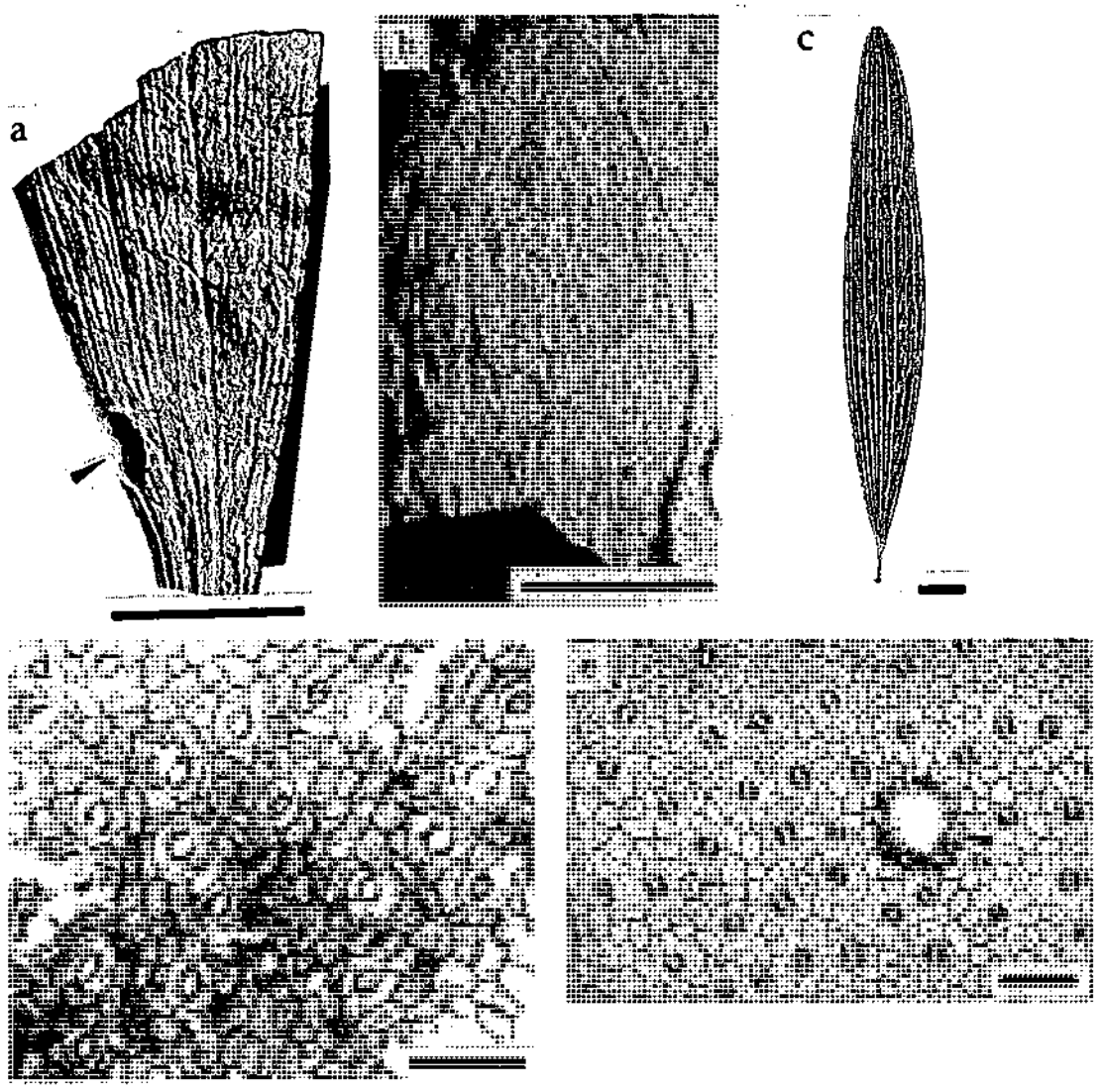


Figure 3.40 : *Acacia*. a, b & d : Fossil *Acacia* sp. nov. from Regatta Point. a : Phyllode base. Note the venation with 2-3 main veins, about 15 more or less parallel veins per cm of width, with occasional reticulations and the prominent nectary (arrow). b : Impression of apex of phyllode to show obtuse apex. d : Cuticle. Note that most stomata have 2 associated uneven sized subsidiary cells, and stomatal axes are more or less parallel. c & e : *A. sophorae*. c : Phyllode. Note the absence of a conspicuous nectary. e : Cuticle. Note the guard cell shape and similar distribution of subsidiary cells to the fossil, but also the prominent gland (arrow). Scale bars for a, b & c = 10 mm, for d & e = 100 µm.

Monimiaceae

***Atherosperma moschatum* (RPU1)**

Specimens examined : RPU 051

Discussion : This taxon (Figure 3.41 a & e) is illustrated by Hill and Macphail (1985). It is indistinguishable in leaf form, venation and cuticle morphology from extant *A. moschatum*. *Atherosperma moschatum* (Figure 4.41 b & f) is a canopy tree of cool temperate rainforest from lowland to moderate altitude in Tasmania and south-eastern Australia, and has no other macrofossil record. It is thought to be moderately well dispersed (e.g. Howard and Ashton 1973; Read 1985).

Myrtaceae

Subfamily Leptospermoideae

The fossil record of the woody fruited Myrtaceae (Leptospermoideae) is quite poor, even though species of this group, particularly species of *Eucalyptus*, *Melaleuca* and *Leptospermum*, are canopy dominants of most vegetation in non arid Australia, and also form major understorey components of many vegetation types. *Eucalyptus* species in Australia require high light conditions for regeneration, and therefore are generally dependent on disturbance, especially fire, for regeneration in closed forest. Members of the Leptospermoideae have small wingless seeds which are enclosed in capsules. These are likely to be poorly dispersed (e.g. more than 95% of seeds fall within a circle of diameter twice the height of *Eucalyptus regnans* trees, (Potts 1990)).

? *Baeckea* (RPU1&ME)

Specimens examined : RPU 365

ME 522-525

Discussion : Fossil leaves (Figure 3.41 d) from the Regatta Point sediments are indistinguishable from extant *Baeckea* (Figure 3.41 c). Fossil leaves and capsules from Melaleuca are also indistinguishable from several species of extant *Baeckea*. *Baeckea* species now occur widely in Australia in sclerophyllous heath communities.

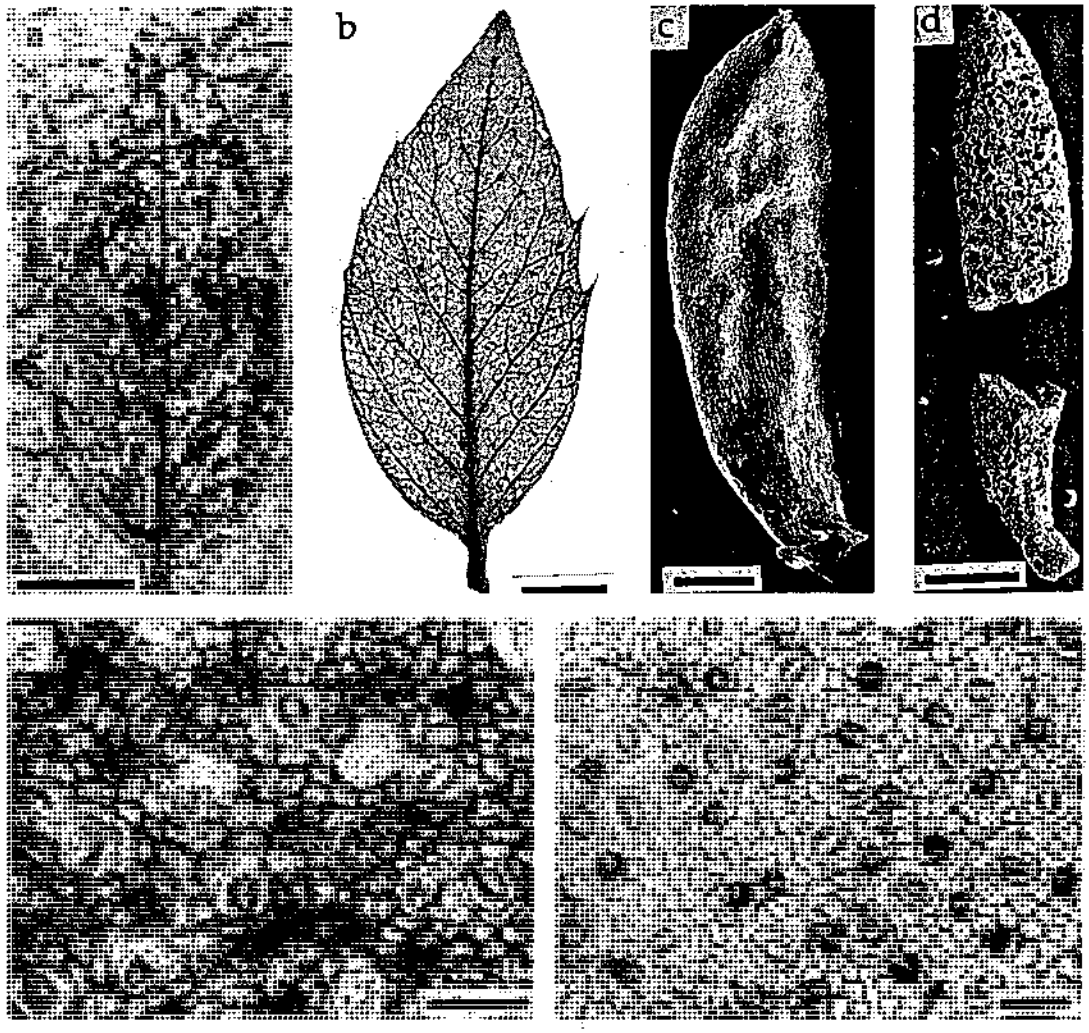


Figure 3.41 : *Atherosperma moschatum* and *Baeckea*. a & e : Fossil *A. moschatum* from Regatta Point. b & f : Extant *A. moschatum*. a & b : Leaves. e & f : Cuticles of stomatiferous surface. c : Extant leaf of *B. gunnianus*. d : Fossil of probable *Baeckea* leaf from Regatta Point. Note the prominent oil glands. Scale bars for a & b = 5 mm, for c & d = 0.5 mm, for e & f = 50 μm.

***Eucalyptus* ? *subcrenulata* (RPU1)**

Specimen examined : RPU 211

Discussion : This fossil (Figures 3.42 a) has leaf form (Figures 3.43) and cuticle (Figure 3.42 c) similar to *E. subcrenulata* (Figure 3.42 b & d). The ovate leaf with intramarginal veins and high angle secondary veins is typical of *Eucalyptus*, and occurs in few non-myrtaceous taxa. Several *Eucalyptus* species have leaf morphology similar to the fossil. Although poorly preserved, the cuticle is indistinguishable from extant *E. subcrenulata* and distinct from *Eucalyptus* species from subgenus *Monocalyptus*. No non-eucalypt species extant in Tasmania has similar leaf form and size. Therefore this fossil is almost certainly a species of *Eucalyptus* and probably of subgenus *Symphyomyrtus*.

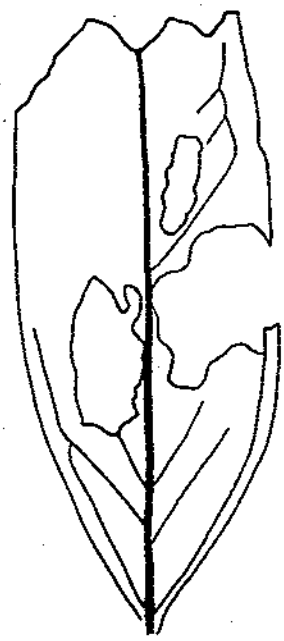


Figure 3.43 : Drawing of fossil *Eucalyptus* ? *subcrenulata* from Regatta Point showing venation. Note the intramarginal vein, slightly irregular margin, and veins diverging from the midrib at about 45°. Compare this with Figure 3.42 b.

Small (about 6 mm diameter) hemispherical capsules consistent with *Eucalyptus* and inconsistent with any extant non-eucalypt Tasmanian species also occur in the Regatta Point sediments. Members of *Eucalyptus* subgenus *Symphyomyrtus* consistent with this fossil are widespread in Australia and range from tall wet forest trees to mallees.

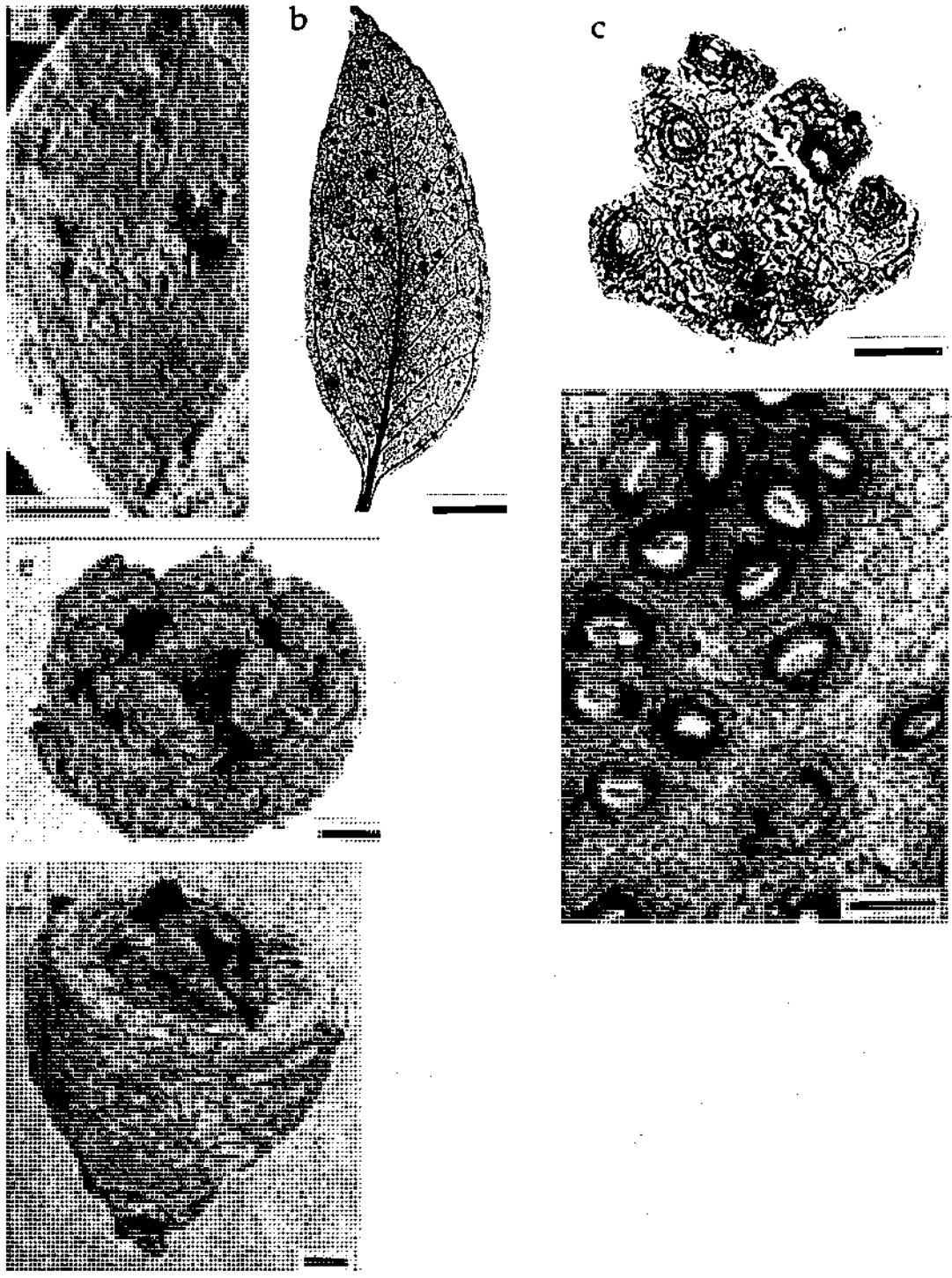


Figure 3.42 : *Eucalyptus*. a : Fossil leaf of *Eucalyptus* ? *subcrenulata* 1. b : Cleared leaf of extant *E. subcrenulata*. c : Cuticle of fossil *Eucalyptus* ? *subcrenulata*. d : Cuticle of extant *E. subcrenulata*. e : Capsule of fossil *Eucalyptus* cf. *subcrenulata* from Regency. Note the three exserted valves (arrow). f : Capsule of extant *E. subcrenulata*. Note the exserted valves (arrow). Scale bars for a & b = 10 mm, for c & d = 50 µm, for e & f = 1 mm.

***Eucalyptus* cf. *subcrenulata* fruit (RE)**

Specimens examined : RE 8117-8149

Discussion : *Eucalyptus* capsules (Figure 3.42 e) occur in the Regency sediments which are morphologically similar to *E. subcrenulata* (Figure 3.42 f), with three exserted valves. These exserted valves occur only in *Eucalyptus*, and are likely to be derived from a *Eucalyptus* subgenus *Symphyomyrtus* species, possibly similar to *E. subcrenulata*. *Eucalyptus subcrenulata* is the only species extant in Tasmania with such woody exserted valves. Other capsules in the sediments may be *Eucalyptus* subgenus *Monocalyptus* fruit. Seeds extracted from these capsules are consistent with *Eucalyptus* and inconsistent with *Leptospermum* which often has similar sized capsules.

***Leptospermum glaucescens* (ME)**

Specimens examined : ME 526-638

Discussion : This fossil taxon was illustrated by Jordan *et al.* (1991). Both fruit (Figure 3.44 a) and leaves (Figure 3.44 c) with cuticle (Figure 3.44 e) indistinguishable from extant *L. glaucescens* (Figures 3.44 b, d & f) occur in the Melaleuca Inlet sediments. The fruit morphology and cuticles of the species of *Leptospermum* extant in Tasmania are all distinctive, and many species can also usually be separated on leaf shape. *Leptospermum glaucescens* is now widespread and common in wet scrub and wet sclerophyll forest from lowland to intermediate altitudes in western Tasmania, and elsewhere.

***Leptospermum nitidum* (ME)**

Specimens examined : ME 539-554

Discussion : This fossil taxon was illustrated by Jordan *et al.* (1991). Both leaves (Figure 3.45 c) with cuticle (Figure 3.45 e) and fruit (Figure 3.45 a) indistinguishable from extant *L. nitidum* (Figures 3.45 b, d & f) occur in the Melaleuca Inlet sediments. *Leptospermum nitidum* is now very common in lowland *Gymnoschoenus sphaerocephalus* sedgeland-heath communities in western Tasmania, and elsewhere.

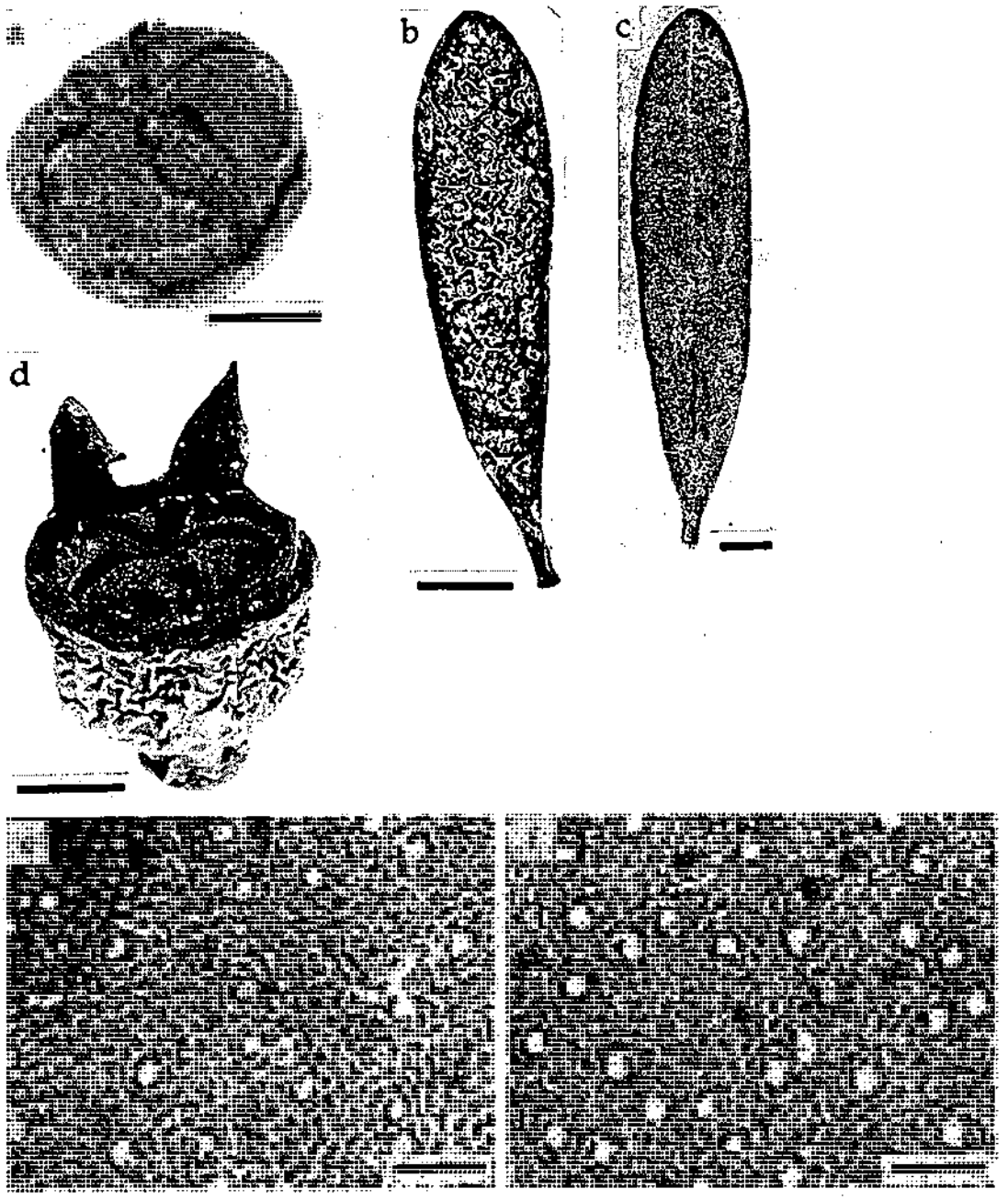


Figure 3.44 : *Leptospermum glaucescens* : a, b & e : Fossils from Melaleuca Inlet. c, d & f : Extant *L. glaucescens*. a & d : Capsules. b & c : Leaves. e & f : Cuticle. Scale bars for a, b, c & d = 1 mm, for e & f = 50 µm.

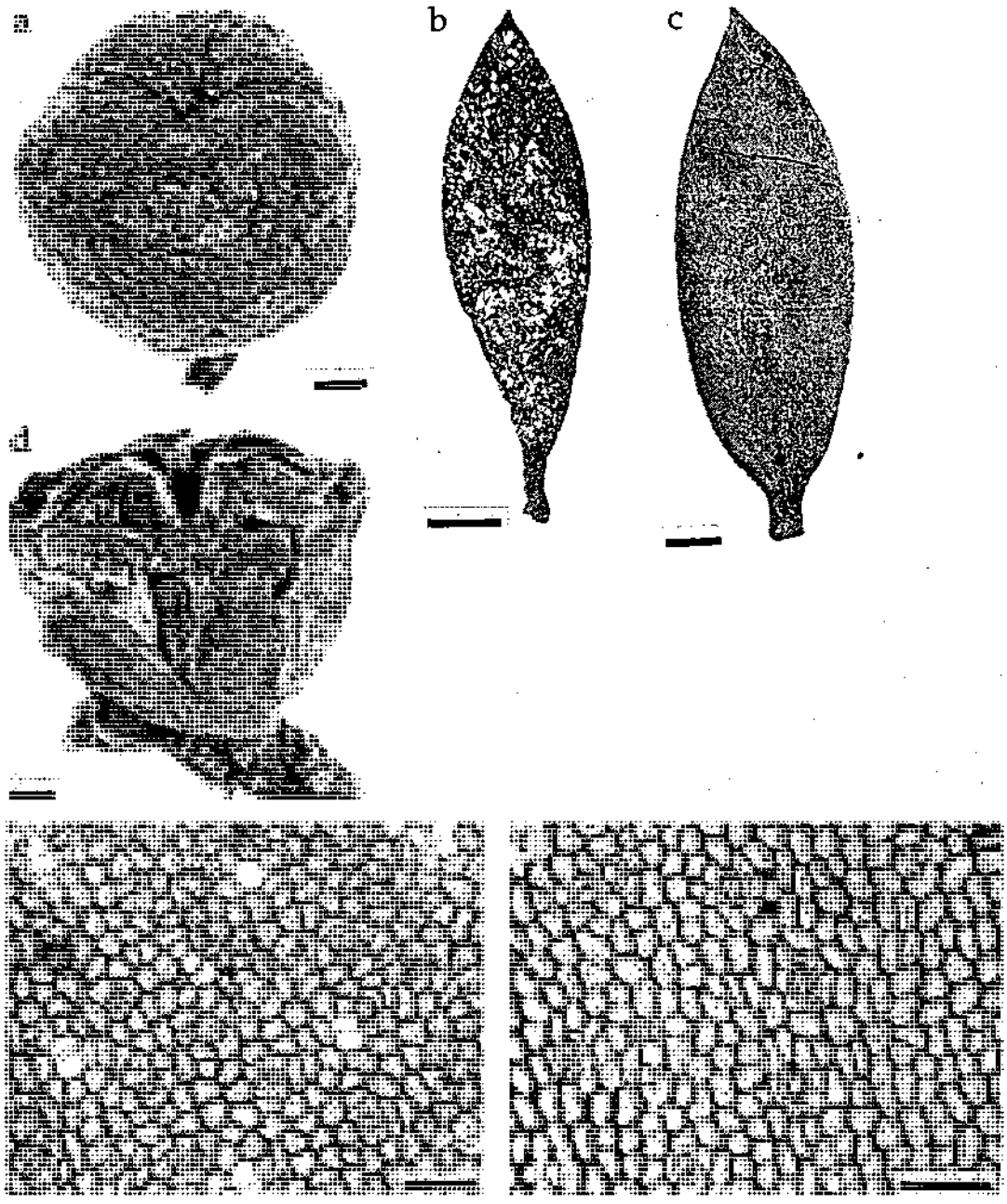


Figure 3.45 : *Leptospermum nitidum*: a, b & e : Fossils from Melaleuca Inlet. c, d & f : Extant *L. nitidum*. a & d : Capsules. b & c : Leaves. e & f : Cuticle. Scale bars for a, b, c & d = 1 mm, for e & f = 50 µm.

***Leptospermum scoparium* (ME); ? *L. scoparium* (RPU1&2)**

Specimens examined : ME 555-571

RPU 490, 1036-1042

Discussion : This fossil taxon was illustrated from the Melaleuca Inlet sediments by Jordan *et al.* (1991). Both leaves (Figure 3.46 c) with cuticle (Figure 3.46 f) and fruit (Figure 3.46 a) indistinguishable from extant *L. scoparium* (Figures 3.46 b, e & g) occur in the Melaleuca Inlet sediments. *Leptospermum scoparium* is now widespread and common in many habitats including sedgeland-heath and wet scrub from lowland to intermediate altitudes. The leaf form of fossils from the Regatta Point sediments (Figure 3.46 e) is similar to *L. scoparium* but is at the small end of its range. The cuticle is consistent with *L. scoparium* but is poorly preserved.

***Leptospermum* sp. (RE)**

Specimens examined : RE 8106-8116

Discussion : Capsules of a probable species of *Leptospermum* occur in the Regency sediments.

***Melaleuca squamea* (ME)**

Specimens examined : ME 572-581

Discussion : This fossil taxon was illustrated by Jordan *et al.* (1991). Leaves (Figure 3.47 a) with cuticle (Figure 3.47 c) indistinguishable from extant *M. squamea* (Figures 3.47 b & d) occur in the Melaleuca Inlet sediments. Fruit consistent with the species also occur in the sediments. *Melaleuca squamea* is now widespread and common in sedgeland-heath and scrub from lowland to subalpine areas. It also occurs in sclerophyll forest.

***Melaleuca squarrosa* (ME)**

Specimens examined : ME 582-609

Discussion : This fossil taxon was illustrated by Jordan *et al.* (1991). Fruit and leaves (Figure 3.47 e) with cuticle (Figure 3.47 g) indistinguishable from extant *M. squarrosa* (Figures 3.47 f & h) occur in the Melaleuca Inlet sediments. *Melaleuca squarrosa* is now widespread and

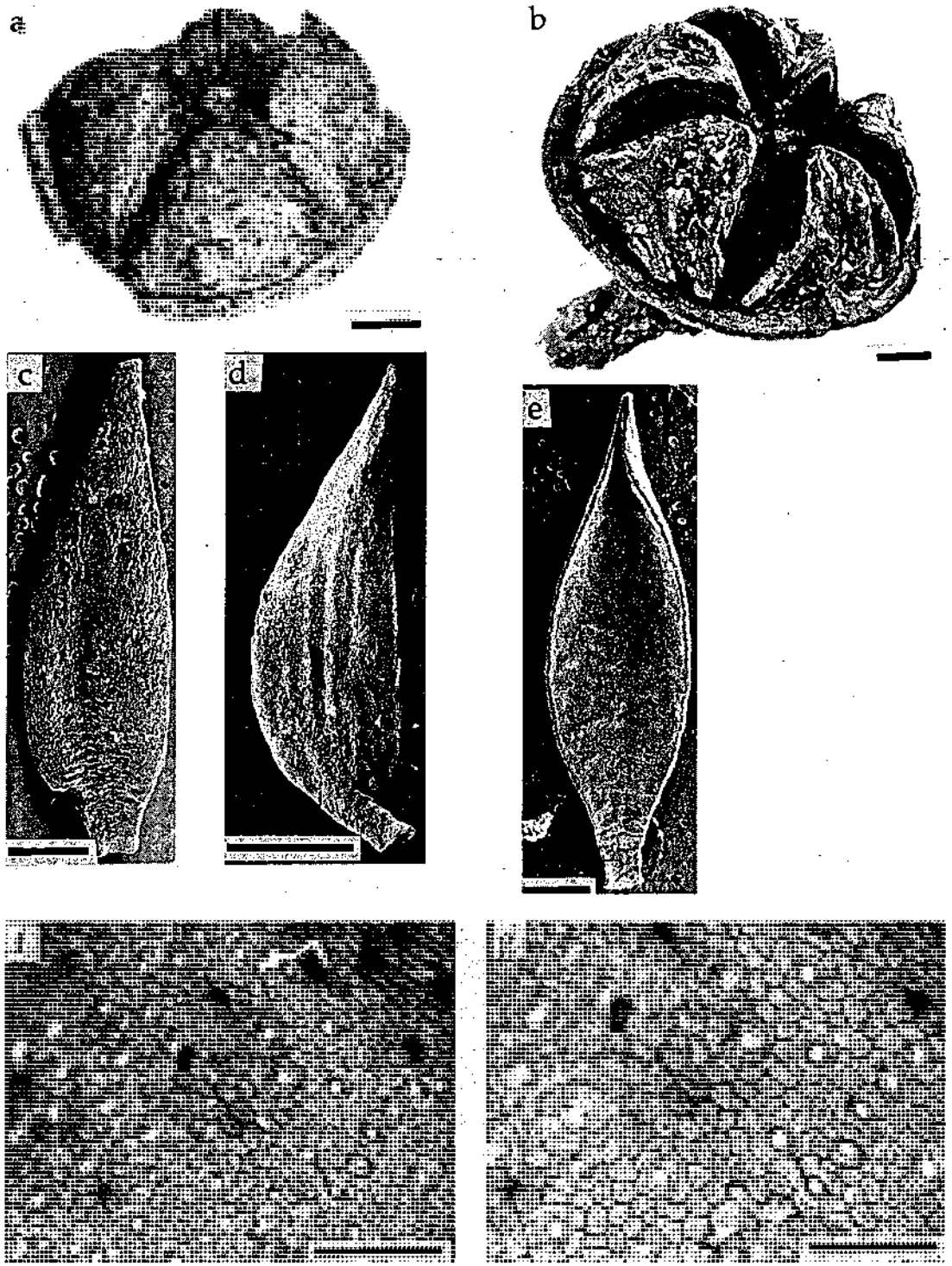


Figure 3.46 : *Leptospermum scoparium* : a, c & f : Fossils from Melaleuca Inlet. b, e & g : Extant *L. scoparium*. d : Fossil ? *L. scoparium* from Regatta Point. a & b : Capsules. c, d & e : Leaves. f & g : Cuticle. Scale bars for a, b, c, d & e = 1 mm, for f & g = 100 µm.

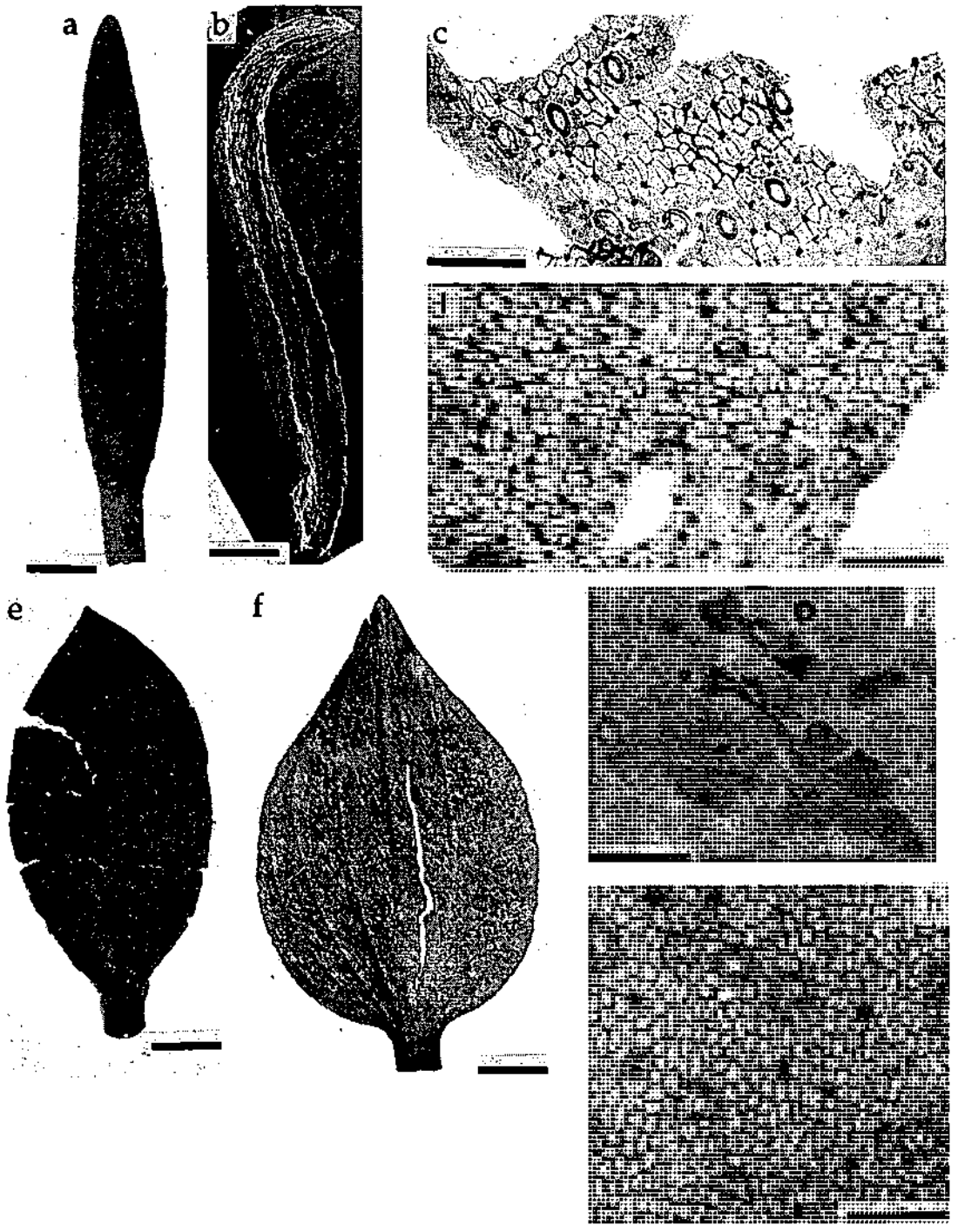


Figure 3.47 : *Melaleuca*. a, b, c, d : *M. squamea*. a & c : Fossil leaf and cuticle from Melaleuca Inlet respectively. b & d : Extant leaf and cuticle respectively. e, f, g & h : *M. squarrosa*. e & g : Fossil leaf and cuticle respectively from Melaleuca Inlet. f & h : Extant leaf and cuticle respectively. Scale bars for a, b, e & f = 1 mm, for c, d, g & h = 100 µm.

common in sedgeland-heath and scrub from lowland to subalpine areas. It also occurs in wet sclerophyll forests.

Subfamily Myrtoideae

aff. *Austromyrtus* (RPU1)

Specimens examined : RPU 468

Description : Leaf petiolate, highly glandular, base obtuse, margins thickened, about 1.5 cm broad. Outer surface of cuticle of non-stomatiferous surface amorphous, except for prominent glands, inner surface isodiametric epidermal cells with sinuous walls, small trichome bases surrounded by a ring of radially elongate cells, glands apparent with lid cells slightly larger and non-sinuous. Inner surface of cuticle of stomatiferous surface with highly sinuous epidermal cell walls, stomata aligned randomly, guard cells broad, larger than epidermal cells, subsidiary cells inconspicuous.

Discussion : The morphology of this fossil (Figure 3.48 a, c & e 3.49 a & c) is consistent in all respects with subfamily Myrtoideae. Lid cells are present on the cuticle (Figure 3.49 a). Lid cells are considered diagnostic of the Myrtaceae (e.g. Christophel and Lys 1986). These are usually pairs of epidermal cells covering glands with a characteristic appearance on the cuticle (Figure 3.49 b). The cuticle morphology is similar to that of some members of *Austromyrtus*. The stomatal shape and distribution (Figure 3.48 c), morphology of the outer surface of the non-stomatiferous cuticle (Figure 3.49 c), trichome bases and sinuous epidermal cell walls (Figure 3.48 e) and shape of the leaf base (Figure 3.48 a) are similar to that of *A. lasioclada* (Figures 3.48 b & d & 3.49 d).

Members of Myrtoideae are widespread, but broad leaved species do not occur in Tasmania, and no extant species with similar cuticle to the fossil occur south of northern N.S.W. (Figure 50). Members of the Myrtoideae have fleshy fruits with resistant seeds which are often eaten by birds and fruit bats, and therefore these species are likely to be well dispersed wherever the birds and fruit bats go. Fossils of broad leaved Myrtoideae are well known from Australian Tertiary sediments (e.g. Christophel and Lys 1986) and including Tasmanian sediments (Hill and Macphail 1983).

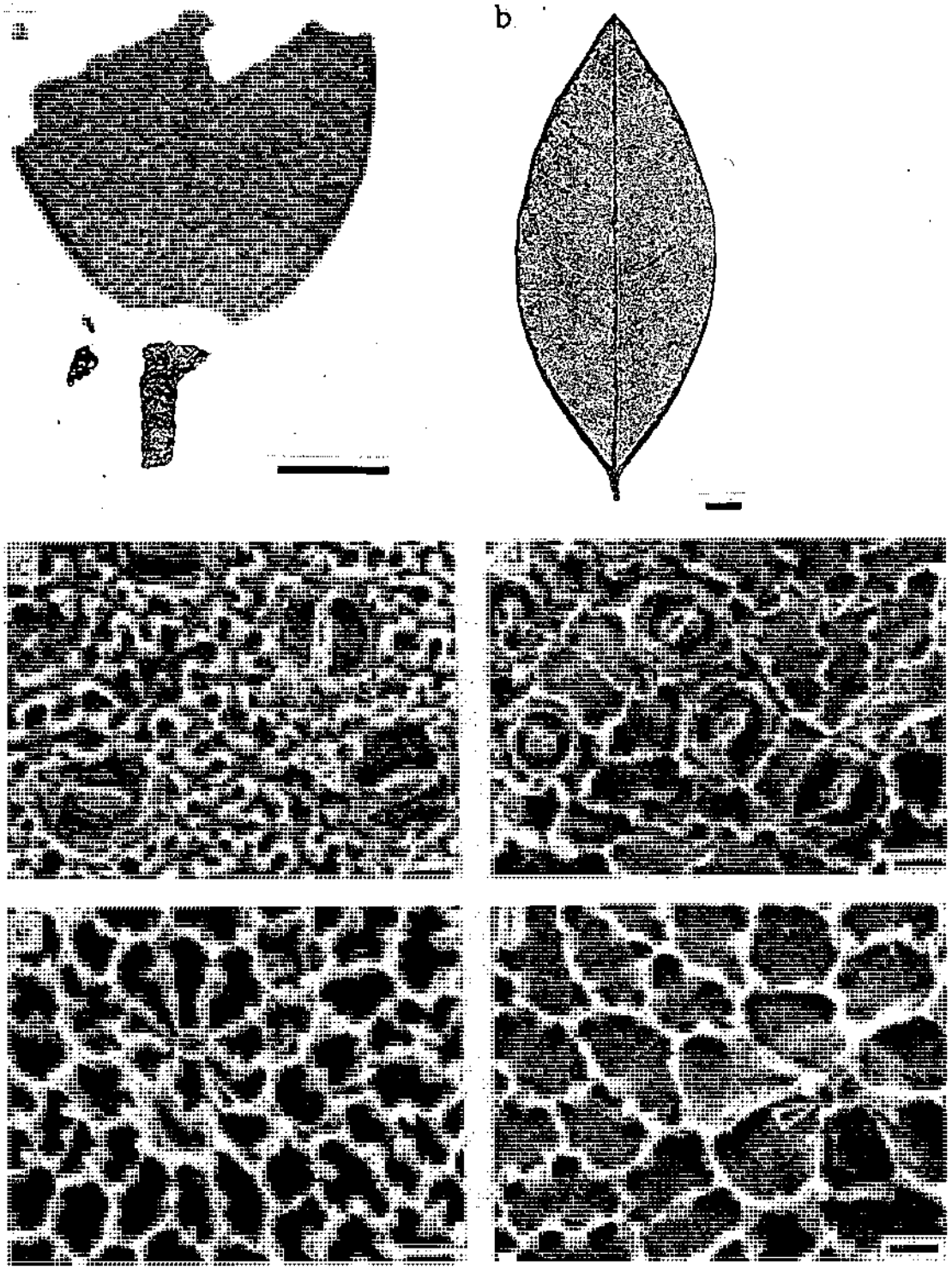


Figure 3.48 : Myrtaceae subfamily Myrtoideae. a, c & e : Fossil cf. *Austromyrtus* from Regatta Point. b, d, & f : *A. lasioclada*. Noté the similarities to the fossil. a : Partial leaf. Note the thickened margin and irregular surface indicating abundant glands. b : Leaf. c & d : Inner surface of cuticle of stomatiferous surface of leaf. Note the sinuous cell walls (more so in the fossil) and nearly circular stomata. e & f : Inner surface of cuticle of non-stomatiferous surface of leaf. Note the trichome bases (arrows). Scale bars for a & b = 5 mm, for c, d, e & f = 10 μm.

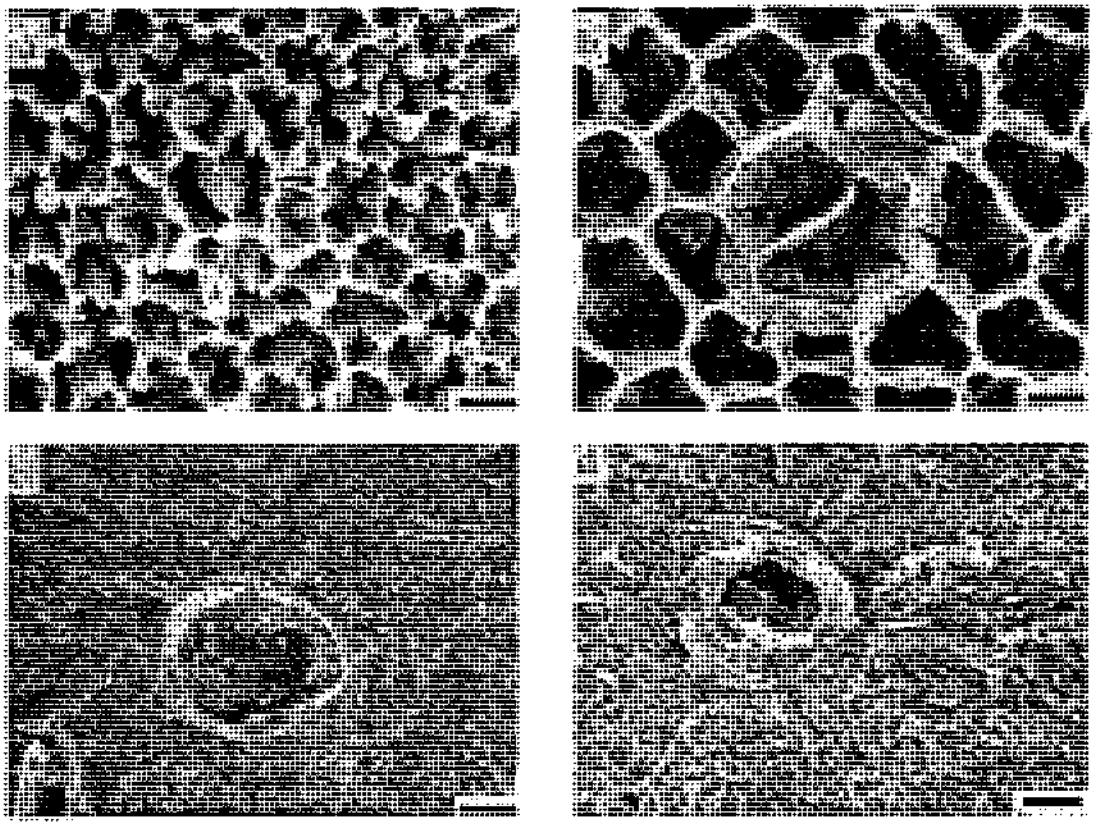


Figure 3.49 : Myrtaceae subfamily Myrtoideae. a & c : Fossil cf. *Austromyrtus* from Regatta Point. b : Extant *A. dallachiana*. a & b : Inner surface of cuticle of non-stomatiferous surface of leaf. Note the lid-cells (arrows). c & d : Outer surface of cuticle of non-stomatiferous surface of leaf showing probable gland. Scale bars = 10 µm.

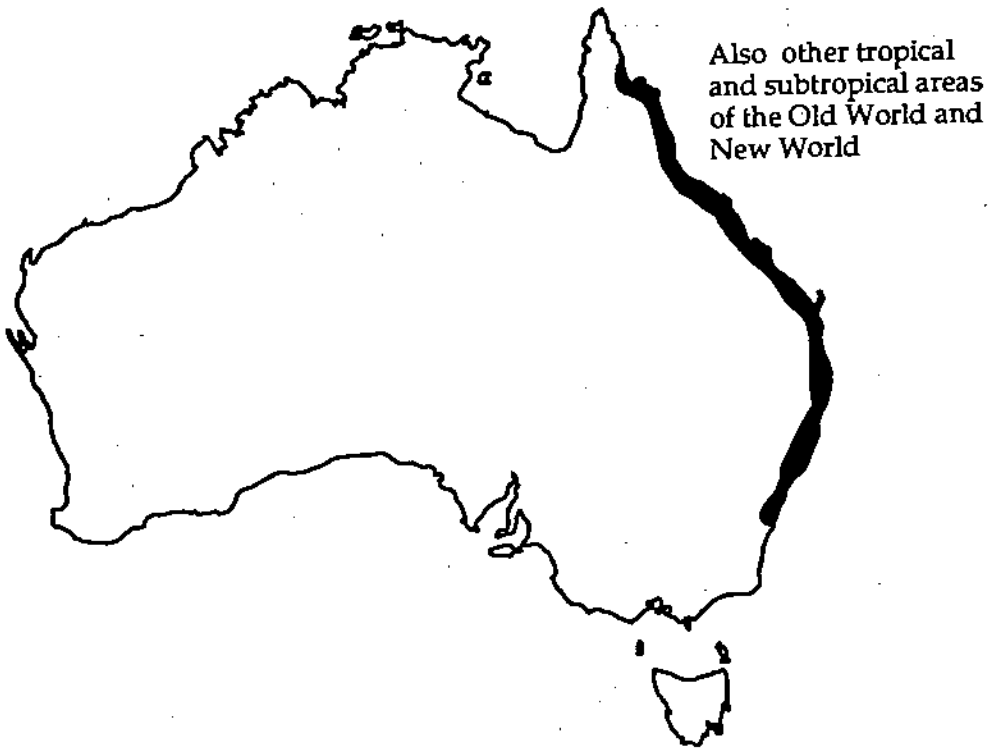


Figure 3.50 : Distribution of *Austromyrtus*. Other broad leaved members of the Myrtoideae have a similar distribution in wet forests on mainland Australia, and also occur in New Zealand and widely in other areas, mainly in wet forests.

Proteaceae

The Proteaceae appear to show considerable morphological convergence in leaf form, so combination of characters are usually necessary to identify fossil taxa. However, the Proteaceae have robust cuticles and strong leaves, and are often well preserved, thus offering a wealth of taxonomic information, and fossil determinations can be strong within this family. The Proteaceae are mainly animal pollinated (Collins and Rebelo 1987). They have either fleshy fruit, winged seeds in dry (often woody) follicles or small nuts (*Agastachys* and a few other genera).

***Agastachys odorata* (RPU1, RE, ME)**

Specimens examined : ME 610-614
RE 8093-8105
RPU 4338-4345

Discussion : This fossil taxon was illustrated from the Melaleuca Inlet sediments by Jordan *et al.* (1991). Large leaf fragments of this species

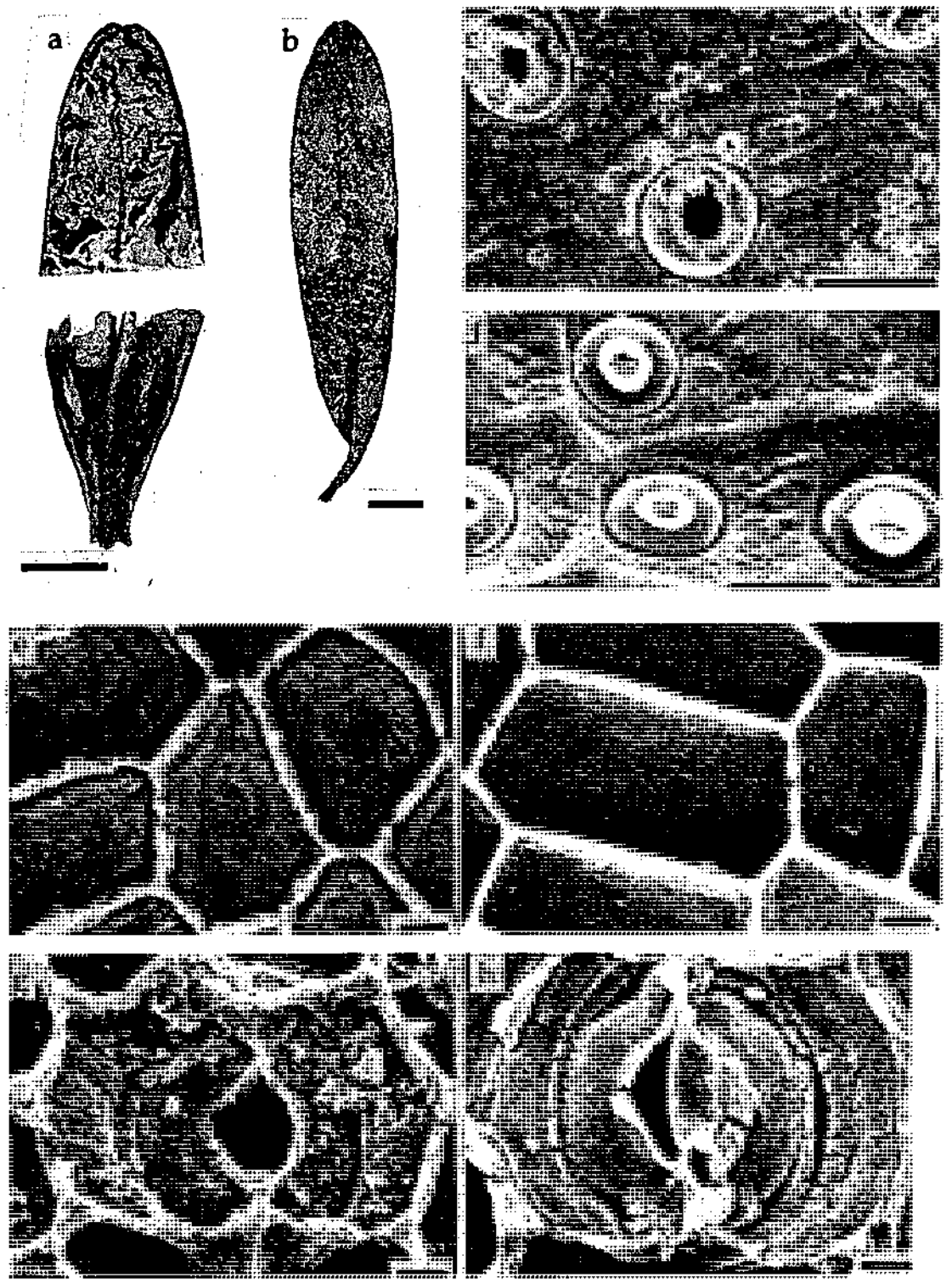


Figure 3.51 : *Agastachys odorata*. a : Fossil leaf fragments from Melaleuca Inlet. b : Extant leaf. c, e & g : Cuticle of fossil from Regatta Point. Note the large size of all cell features compared with other Proteaceae (e.g. Figures 58, 60, 63 & 66). d, f & h : Cuticle of extant *A. odorata*. c & d : Outer surface of stomatiferous surface. e & f : Inner surface of non-stomatiferous surface. g & h : Inner surface of stomatiferous surface. Scale bars for a & b = 5 mm, for c & d = 50 µm, for e, f, g & h = 10 µm.

occur in the Regency and Melaleuca Inlet sediments (Figure 3.51 a). The cuticle from these fragments is well preserved and is identical to that of extant *A. odorata* (Figures 3.51 d, f & h). Only cuticle fragments of this species are known from the Regatta Point sediments (Figures 3.51 c, e & g), but these are indistinguishable from extant *Agastachys odorata* which has highly distinctive cuticle. The very large regular epidermal, and stomatal cells of both surfaces, and stomatiferous surface with paratetracytic stomates aligned with the main leaf axis with prominent T-pieces of cuticle at the stomatal poles are characteristic of the species. The cells apparent on the cuticle are larger than the comparable cells of any dicotyledonous species in the extensive collection held in the Plant Science Department at the University of Tasmania. *Agastachys odorata* is common in Tasmanian Pleistocene macrofossil bearing sediments, but the genus is unknown from the Tertiary. *Agastachys* is a monotypic genus endemic to Tasmania. *Agastachys odorata* occurs in westem, south-western and southem areas and is primarily a shrub in sedgeland/heath but extends into wet forest and rainforest as small tree. It has small winged nut which is unlikely to be well dispersed.

Banksia

Only two extant species of *Banksia* occur naturally on mainland Tasmania. *Banksia marginata* is widespread and *B. serrata* is restricted to a small area of northwest Tasmania (Taylor and Hopper 1988). However, three species of *Banksieaephyllum* and one species of *Banksieaeformis* have been described from Eocene and Oligocene sediments in Tasmania (Hill and Christophel 1988). Also, four undescribed species of *Banksieaephyllum* and two of *Banksieaeformis* have been recovered from the Oligocene Cethana sediments, although one of the species of *Banksieaeformis* may be the same as one of the species of *Banksieaephyllum* (Carpenter 1991). These taxa cover a wide range of forms and their affinities at the subgeneric level are uncertain. *Banksieaephyllum* encompasses organically preserved fossil leaves consistent with the sub-tribe Banksieae (Cookson and Duigan 1950). Banksieae encompasses the extant genera *Banksia*, now widespread in Australia, and *Dryandra*, now restricted to south-west Australia, and the two

small North Queensland rainforest genera *Musgravea* and *Austromuellera* (Johnson and Briggs 1975). *Banksieaeformis* is used to describe leaves with architecture consistent with Banksieae but without cuticular preservation (Hill and Christophel 1988). Most *Banksieaephyllum* species are clearly more closely related to *Banksia* or *Dryandra* than to *Austromuellera* or *Musgravea* (e.g. Hill and Christophel 1988). There are no Tasmanian Miocene or Pliocene macrofossil records of the Banksieae, but there is a paucity of macrofossil bearing sediments of these ages. It is clear that there were many kinds of *Banksia* or close relatives in Tasmania in the early Tertiary and that almost all of these are now extinct, but it is not clear when these extinctions occurred. *Banksia* species have relatively large seeds (about 1-4 cm long) with papery wings and are likely to be dispersed only short distances (George 1984). The taxonomic descriptions and discussions of *B. kingii, B. strahanensis* and the probable *B. kingii* infructescences from the Melaleuca Inlet sediments are extracted from Jordan and Hill (1991) (Appendix 3).

***Banksia kingii* (ME)**

Specimens examined : ME-001 to ME-030 (Leaves)

Description : Leaves linear-obovate, bifacial, about 1 cm wide and 12 cm long, very thick, with thick revolute margins. Stomatiferous surface with secondary veins diverging at about 60° from the robust midrib, tertiary veins forming a prominent reticulate network. Apex very narrowly emarginate. Petiole 2-3 mm wide, about 2 mm thick, 4-6 mm long. Cuticle of non -stomatiferous surface with cells nearly isodiametric, 4-7 sided, irregularly arranged with porose walls, trichome bases of 1-4 rounded, slightly enlarged cells with thicker cuticle. Cuticle of stomatiferous surface with stomates in irregular shaped, trichome filled pits of width exceeding the distance between them and comprising the areoles between the lowest order veins. Cells between pits small, ± rhomboidal, with porose walls and almost all bearing a central trichome.

Discussion : This fossil taxon was described and illustrated by Jordan *et al.* (1991 appendix 1). *Banksia kingii* is illustrated in Figures 3.52 a & e

3.53 a & c. For comparison *Banksia saxicola* is illustrated in Figures 3.52 b & f & 3.53 b & d, *B. canei* in Figures 3.52 c & h & 3.53 g, *B. plagiocarpa* in Figures 3.52 g & 3.53 e and *B. marginata* in Figure 3.53 f. The robust symmetrical bilateral leaves with revolute margins and prominent mibribs of *Banksia kingii* are typical of subtribe Banksiinae and within this subtribe entire leaves with prominent reticulate venation on the stomatiferous surface occur only in *Banksia* series *Salicinae* (George 1981). The cuticle of *Banksia kingii* is consistent in cell shape, trichome base form and stomatal distribution and form with *Salicinae*. Leaves of similar shape and size to *Banksia kingii* occur in *B. integrifolia* var. *compar*, *B. plagiocarpa* and some large leaved forms of *B. marginata* and *B. canei*. The fossil leaves are more robust than the leaves of any of these taxa, in that they have more sclerified tissue, thicker laminas, cuticles, midribs, margins and petioles. In particular they are much more robust than the leaves of *Banksia integrifolia* var. *compar* and any forms of *B. marginata* or *B. canei* which have leaves of similar size to those of *B. kingii*. Only *B. saxicola* and *B. plagiocarpa* have forms which are of similar size and approach the robustness of *B. kingii*. The cuticle of the stomatiferous surface of *Banksia kingii* differs from all these taxa in pit sizes, cell sizes and shapes and/or in the form and distribution of trichome bases. It differs from *B. saxicola* (Figure 3.52 f) only in having larger pits. However, *B. saxicola* has elliptic to obovate leaves (Figure 3.52 b) whereas *B. kingii* has linear obovate leaves (Figure 3.52 a). *Banksia plagiocarpa*, which is similar to *B. kingii* in leaf shape, differs significantly in cuticular characters of the stomatiferous surface in having larger trichome bases placed on small, nearly isodiametric cells and smaller pits (Figure 3.52 g). *Banksia canei* has smaller pits than *B. kingii* and between the pits it has larger cells which rarely have trichome bases (Figure 3.52 h). *Banksia kingii* thus differs from all extant species in both microscopic and macroscopic features and requires specific status. It can, however, be allied to *B. canei* and particularly *B. saxicola* on the basis of shared cuticular characters.

B. saxicola occurs in two disjunct areas of Victoria (Figure 3.55) : in the Grampian Ranges from moderate altitudes to subalpine areas, in woodlands on the depauperate sandstone soils of this area, and on

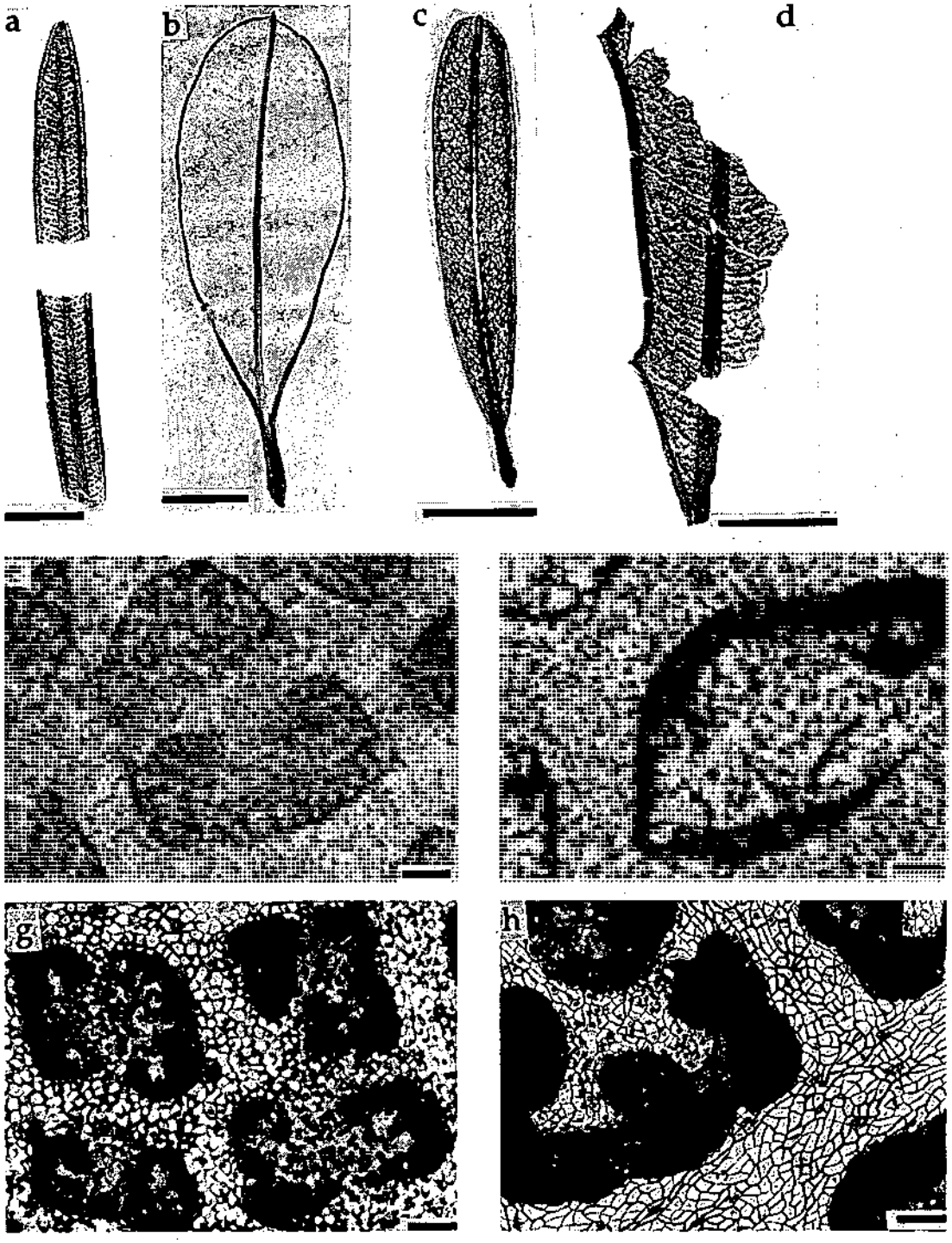


Figure 3.52. *Banksia* Series *Salicinae*. a & e : Fossil *B. kingii* from Melaleuca Inlet. b & f : Extant *B. saxicola*. c & h : Extant *B. canei*. d : Fossil *B.* cf. *kingii* from Regatta Point. g : Extant *B. plagiocarpa*. a, b, c & d : Leaves. e, f, g & h : Cuticles of stomatiferous surface. Scale bars for a, b, c & d = 10 mm, for e, f, g & h = 100 μm.

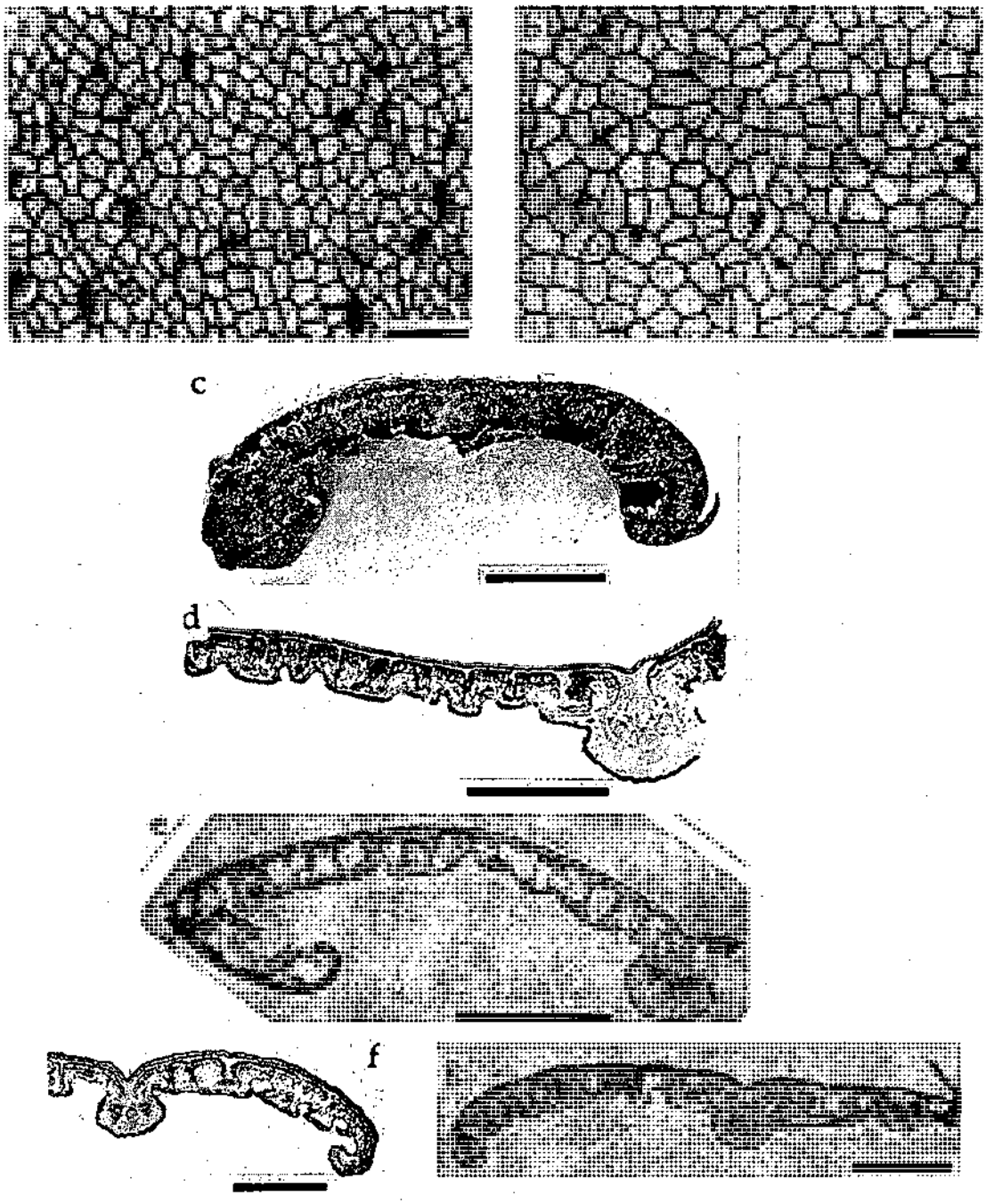


Figure 3.53. *Banksia* Series *Salicinae*. a : Cuticle of non-stomatiferous surface of fossil *B. kingii* from Melaleuca Inlet. b : Cuticle of non-stomatiferous surface of *B. saxicola*. c, d, e, f & g : Transverse sections of leaves. c : Fossil *B. kingii* from Melaleuca Inlet. d : Extant *B. saxicola*. e : Extant *B. plagiocarpa*. f : Extant *B. marginata*. g : Extant *B. canei*. Scale bars for a & b = 100 µm, for c, d, e & f = 1 mm.
* Thick section

Wilson's Promontory at low altitudes in forest, on the siliceous granite soils. *B. canei* occurs in the subalpine woodlands of southern New South Wales and Eastern Victoria on granitic or sandstone soils (Figure 3.55).

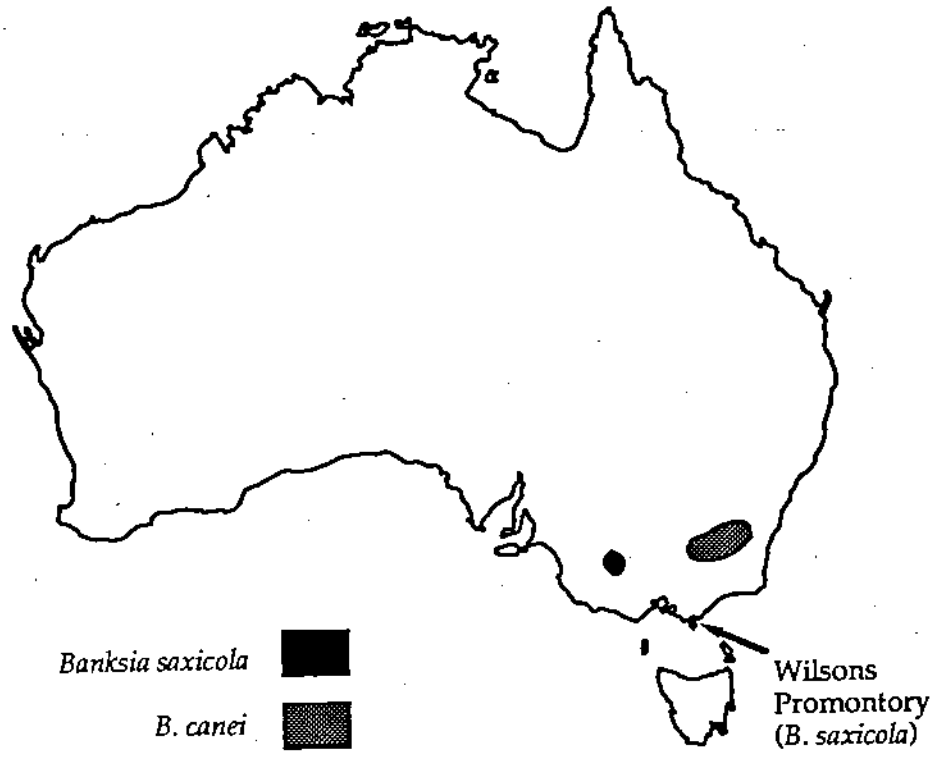


Figure 3.55. Extant distribution of *Banksia saxicola*, *B. canei*.

***Banksia ? kingii* infructescences**

Specimens examined : ME 031-034

Description : Infructescence cylindrical, 62 mm long, 46 mm wide including follicles, axis robust. Styles and perianths absent. Common and floral bracts compactly arranged, eroded to an even height of 4 mm, separated by dark brown trichomes. Common bracts diamond shaped, 3 mm x 2 mm. Floral bracts oblong 1.5-2 mm x 1 mm. Follicles oblong in plan view, robust and highly exserted, 11-14 mm wide, 6-7 mm thick, 5-6 mm high, perpendicular to cone axis, sparse and irregularly arranged on cone axis, some remaining closed. Valves semicircular-elliptic, nearly oblong in section. Ridge wide and obtuse. Separator about 10 mm wide, wings 8 mm x 1.5 mm.

Discussion : This fossil taxon was described and illustrated by Jordan

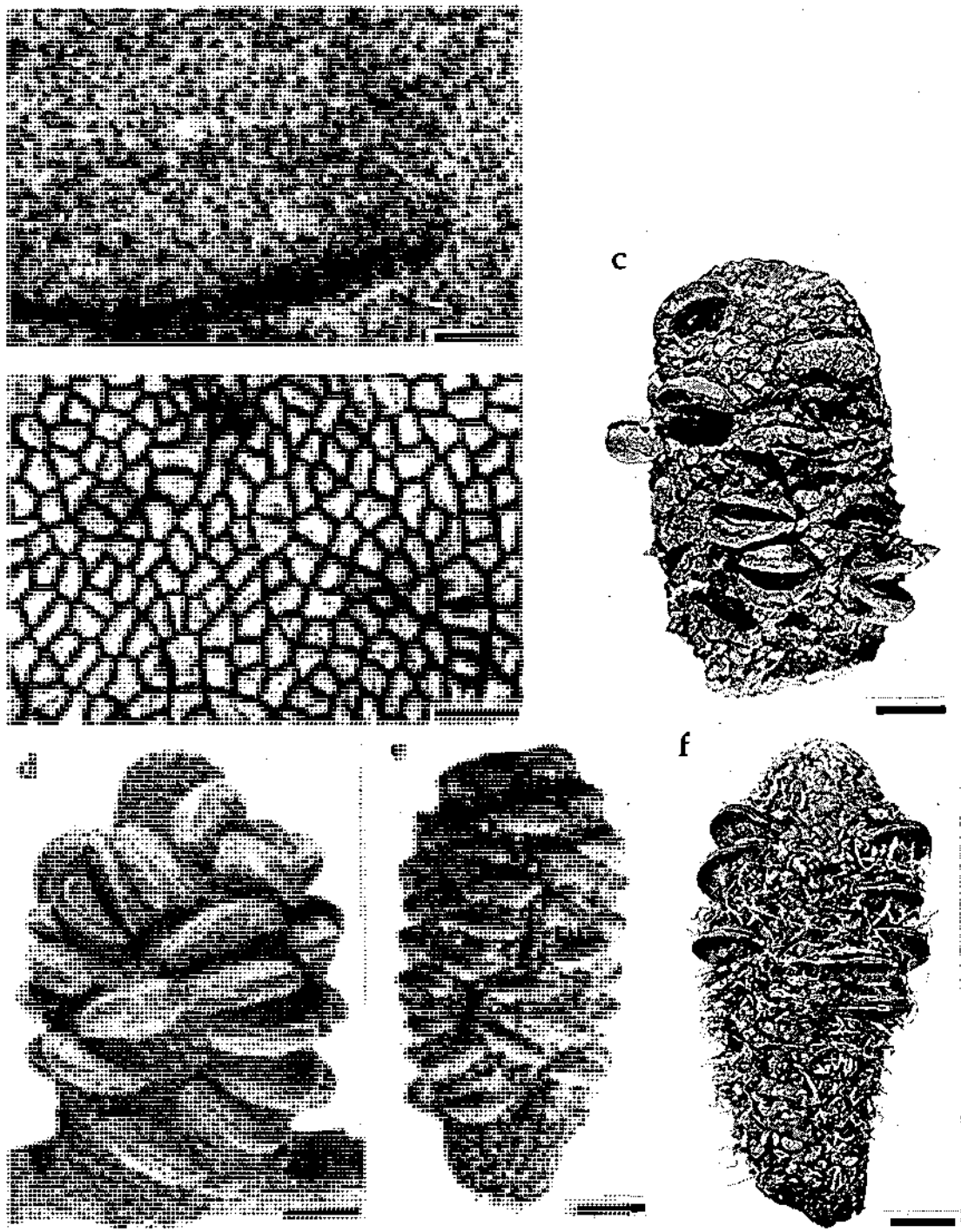


Figure 3.54. *Banksia* Series *Salicinae*. a & b : Cuticle of fossil *B.* cf. *kingii* from Regatta Point. Note the similarity with Figures 3.52 e & 3.53 a. a : Stomatiferous surface. b : Non-stomatiferous surface. c, d, e & f : Infructescences. c : Probable *B. kingii* fossil from Melaleuca Inlet. d : Extant *B. saxicola*. e : Extant *B. canei*. f : Extant *B. marginata*. Scale bars for a & b = 100 µm, for c, d, e & f = 10 mm.

et al. (1991). The fossil infructescence (Figure 3.54 c) is morphologically closest to that of *B. saxicola* (Figure 3.54 d) but is more robust and has more exserted and robust follicles, which in *B. saxicola* are semicircular-elliptic in section. The fossil is also related to *B. marginata, B. canei* and *B. integrifolia. Banksia marginata* (Figure 3.54 f) is highly variable, but the fossil infructescence has a more robust axis, it has early deciduous styles, the follicles are more robust, more exserted, with a thicker ridge and are nearly oblong in plan view and section. Some forms of *B. marginata* appear to have early deciduous styles, that is the styles of carpels with unfertilized ovaries are shed soon after the fertilization of other ovaries, but dissection of the common and floral bracts invariably exposes the lower parts of the styles. Dissecting out the common and floral bracts of the fossil exposes well preserved densely packed trichomes with no styles or gaps for styles. The fossil has more exserted, oblong follicles, thicker follicle ridges and narrower separators than *B. canei* (Figure 3.54 e). In *B. canei* the separator has wings nearly as wide as the follicle, whereas those of the fossil are narrow. The fossil has much more robust follicles and infructescence axes than *B. integrifolia* which has follicles which are semicircular-elliptic in section, have narrow ridges and all open at maturity.

These infructescences are consistent with a species closely related to *B. saxicola* and *B. canei*, but are sufficiently distinct to warrant specific status. They therefore have similar taxonomic affinities to the *B. kingii* leaves. The leaves of *B. kingii* and the infructescences were extracted from different lenses at the same site, but are of similar ages. Therefore, while there is no direct organic or stratigraphic connection between the two types, the taxonomic similarity and the similarity of age to the *B. kingii* leaves seem sufficient for the fruits to be ascribed to *B. kingii.*

***Banksia* cf. *kingii* (RPU1)**

Specimens examined : RPU 464

Discussion : This species is known from only one incomplete leaf (Figure 3.52 d & 3.54 a & b). It is clearly a member of series *Salicinae.* Its cuticle morphology (Figures 3.54 a & b) is very similar to that of *B. saxicola* (Figures 3.52 f & 3.53 b)and the extinct *B. kingii* (Figures 3.52 e & 3.53 a)

described in Jordan and Hill (1991).The single leaf has teeth and is broader than the known *B. kingii* leaves. It is, however, very thick like *B. kingii* and unlike large leaved forms of *B. saxicola*. All extant members of *Banksia* series *Salicinae* usually have juvenile leaves which are toothed and broader than their adult leaves (George 1981). The ranges of adult leaves of most species of series *Salicinae*, including normally entire leaved species, cover broad size ranges and include toothed forms. This fossil *Banksia* from the Regatta Point sediments is therefore not inconsistent with *B. kingii*. It differs from the species of *Banksia* extant in Tasmania, *B. marginata* and *B. serrata*, in leaf form and cuticle characters. *B. marginata* is never as large and as robust at the same time, as the fossil, and *B. serrata* has regularly serrate margins and stomata restricted to small deep pits, whereas the fossil has stomata in broad shallow pits. The fossil is therefore from a species extinct from Tasmania, but closely related to species from mainland Australia.

Banksia strahanensis **(RPU1&2)**

Specimens examined : RPU 022-025, 380, 381, 405-408, 445, 483, 4346-4364

Description : Leaf linear, bifacial, entire, obtuse and mucronate, 2-3 mm wide, about 40 mm long, petiole 3.5 - 4 mm long, margins thick and revolute, non-stomatiferous surface sparsely hairy, stomatiferous surface with prominent midrib, lamina between margin and midrib exposed and densely hairy. Cuticle of non-stomatiferous surface with roughly isodiametric cells without papillae or ribbing, 1-3 celled trichome bases of rounded, slightly enlarged cells present. Cuticle of stomatiferous surface with lamina between midrib and each margin uniformly composed of superficial stomates evenly interspersed with rhomboidal cells bearing single trichome bases and with porose cell walls except near the margins and midrib, where all cells bear single trichome bases. Cuticle of midrib of elongate, thick walled cells with occasional 1-2 celled trichome bases.

Discussion : This fossil taxon was described and illustrated by Jordan *et al.* (1991 appendix 1). *Banksia strahanensis* is illustrated in Figures 3.56

a, c, e & g and *B. spinulosa* Smith is illustrated for comparison in Figures 3.56 b, d, f & h. The cuticular and leaf morphology of the fossil place it readily in subtribe Banksiinae. Narrow entire leaves and the absence of apparent reticulate venation on the stomatiferous surface occur only in section *Oncostylis* of *Banksia* (George 1981) and do not occur in *Dryandra*. *Banksia strahanensis* is compared with all the extant members of *Oncostylis* in Table 3.1. Section *Oncostylis* is composed of three series : *Spicigerae*, which includes *B. spinulosa* and *B. ericifolia* from south-eastern Australia and other species all from south-west Western Australia, and series *Abietinae* and *Dryandroideae*, which are restricted to south-west Western Australia. *B. strahanensis* is clearly a member of series *Spicigerae*. Series *Dryandroideae*, which contains only *B. dryandroides*, differs in having leaves with deep triangular lobes and cuticular ribs connecting trichome bases on the inner surface of the cuticle of the non-stomatiferous surface. These ribs are highly distinctive features of *B. dryandroides* and some species of series *Abietinae*. Series *Abietinae* is characterised by very narrow entire leaves with strongly revolute margins and, with the exception of *B. nutans*, nearly isodiametric cuticular cells of the non-stomatiferous surface. *Banksia strahanensis* has slightly wider, less revolute leaves than members of series *Abietinae* and elongate cuticular cells of the non-stomatiferous surface. *Banksia strahanensis* also differs from most taxa of series *Abietinae* in having the stomatiferous area of the cuticle densely and evenly covered with trichome bases, and in having no ribs between trichome bases on the cuticle of the non-stomatiferous surface.

Banksia strahanensis is consistent with series *Spicigerae* in all characters except that it shows no evidence of venation on the cuticle of the stomatiferous surface. The cuticles of the stomatiferous surface of all members of section *Oncostylis* have areas of the lamina over veins without stomates (Figure 3.56 f). This does not occur in *Banksia strahanensis*. *Banksia strahanensis* falls within the range of *B. spinulosa*, particularly var. *spinulosa*, except in this character, in having a longer petiole and the combination of narrow, very revolute leaves without cuticular papillae. Forms of *Banksia spinulosa* with leaves as narrow as those of *B. strahanensis* have abundant cuticular papillae on the non-stomatiferous

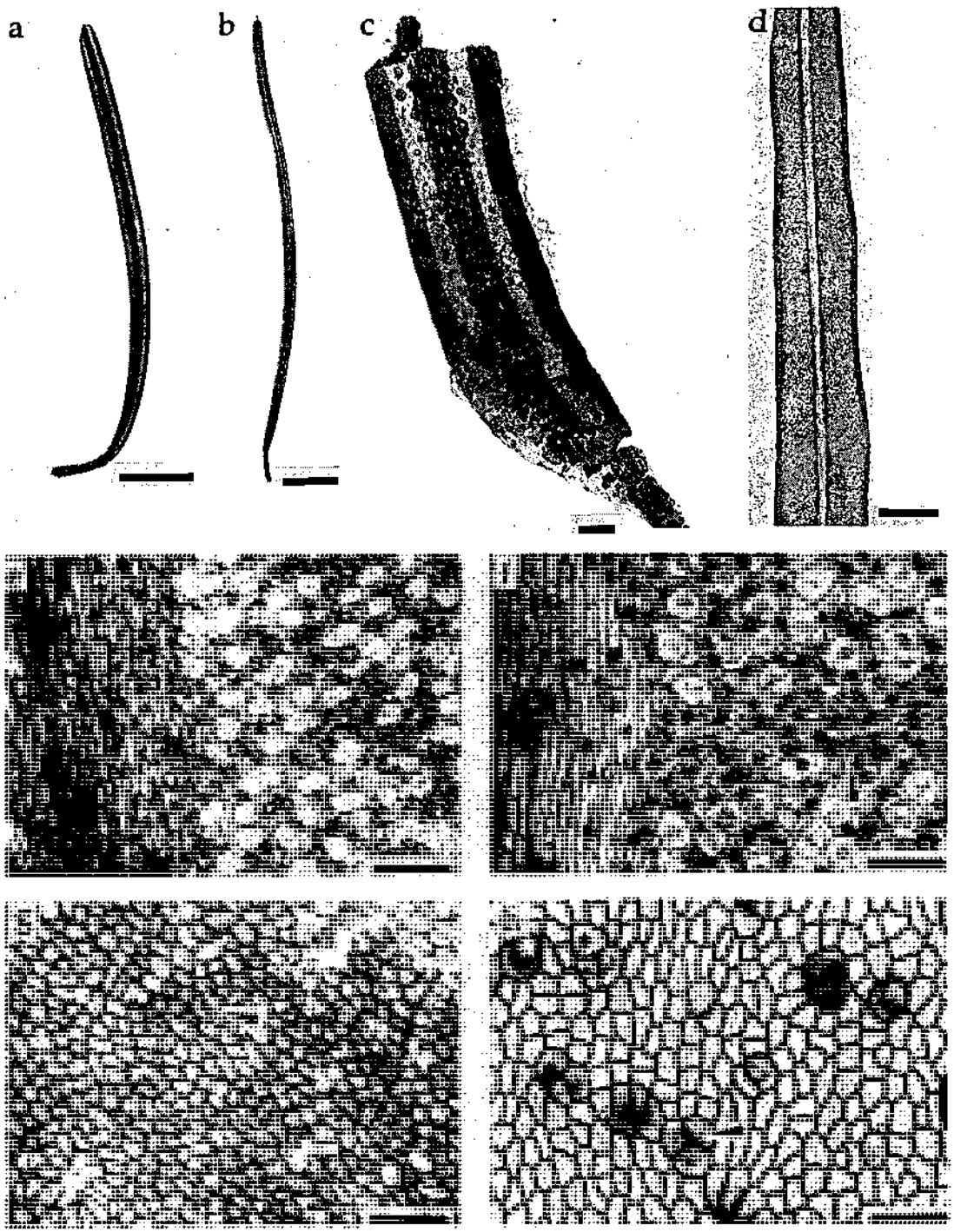


Figure 3.56 : *Banksia* series *Spicigerae*. a, c, e & g : Fossil *B. strahanensis* from Regatta Point. b, d, f & h : Extant *B. spinulosa*. a & b : Leaves. c & d : Leaf fragments. Note the prominent midrib and revolute margins. e & f : Cuticles of stomatiferous surfaces. The left hand section of cuticle without stomata covers the midrib. Note the even distribution of stomata over the lamina of the fossil and compare this with f and Figure 3.52 e, f, g & h. Note the area of lamina without stomata (arrow) in the extant species. g & h : Cuticle of non-stomatiferous surface. Note the trichome bases (arrows). Scale bars for a & b = 5 mm, for c & d = 2 mm, for e & f = 100 µm.

Series	Species	leaf form characters							cuticle characters					
		leaf shape	margin shape	revolute margin	leaf width (mm)	leaf length (cm)	petiole length (mm)	apex shape	papillae	cell size	cell shape	laminar hairs	veins	ribs
Fossil	*B. strahanensis*	linear	entire	+	2-2.5	4	3.5-4	obtuse	-	small	long	dense	-	-
Spicigerae	*B. spinulosa*	linear	±serrate	±	1.5-11	3-11	1-3	±obtuse	±	small	long	dense	+	-
"	*B. ericifolia*	linear	entire	++	0.8-1.5	0.9-2	1-2	3 toothed	+	small	long	dense	+	-
"	*B. brownii*	elliptic	lobed	+	3-5	3-11	2-5	retuse	+	large	long	dense	+	-
"	*B. occidentalis*	linear	±serrate	+	2-3	4-13	1-5	truncate	+	large	short	dense	+	-
"	*B. littoralis*	linear	entire	-	4-10	10-23	5-10	±obtuse	+	small	long	dense	+	-
"	*B. seminuda*	linear	entire	-	4-18	5-12	5-10	±obtuse	+	small	long	dense	+	-
"	*B. tricuspis*	linear	entire	++	1-1.5	5-13	2-5	obtuse	-	small	short	+	+	-
"	*B. verticillata*	elliptic	±serrate	-	7-12	3-9	5-11	obtuse	+	large	short	dense	+	-
Abietinae	*B. nutans*	linear	entire	++	0.5-1.3	1-2.8	2-3	acute	+	large	long	+	+	-
"	*B. grossa*	linear	entire	++	1.8-2.8	4-12	3-5	obtuse	+	small	short	absent	+	+
"	*B. incana*	linear	entire	++	1.5-2	1-6	1-2	acute	+	small	short	+	+	(+)
"	*B. lanata*	linear	entire	++	0.7-1	3-10	3-4	acute	+	small	short	+	+	-
"	*B. laricina*	linear	entire	++	± 0.8	0.5-1.5	1-1.5	acute	+	small	short	+	+	+
"	*B. leptophylla*	linear	entire	++	1-1.5	4-10	1-2	acute	±	small	short	+	+	(+)
"	*B. meisneri*	linear	entire	++	1-1.5	0.3-1.5	0.5-1	obtuse	-	small	short	+	+	-
"	*B. micrantha*	linear	entire	++	1-1.5	1-3	2-3	acute	+	small	short	absent	+	-
"	*B. pulchella*	linear	entire	++	1-1.5	0.4-1.3	1-1.5	obtuse	+	small	short	+	+	+
"	*B. scabrella*	linear	entire	++	±1	0.8-3	1-2	acute	+	small	short	dense	+	+
"	*B. sphaerocarpa*	linear	entire	++	1.5-2	2.5-10	2-3	acute	+	small	short	+	+	+
"	*B. telmatiaea*	linear	entire	++	1-1.3	1.5-4	1.5-2	obtuse	+	small	short	dense	+	+
"	*B. violacea*	linear	entire	++	±1.5	1-2	1-2	±obtuse	+	small	short	+	+	(+)
Dryandroideae	*B. dryandroides*	linear	lobed	++	7-15	5-17	<1	truncate	-	small	short	dense	+	+

Table 3.1 : Leaf and cuticle morphological characters of species of *Banksia* section *Oncostylis* Benth. including *B. strahanensis* Jordan & Hill sp. nov. The information is this table is derived from this study and George (1981). In the column "margin shape", "entire" means the leaf margin is entire for most of its length. In the column "revolute margin", "-" means recurved margin, "+" means revolute margin, "++" means strongly revolute margin. In other columns + means present, - means absent, (+) means present but poorly developed and ± means more or less, or either pesent or absent. In the column "cell size" small is mean cell width <35 µm; large is mean cell width >45 µm. In the column "cell length" short is mean cell length : mean cell width < 1.5 : 1 ; long is mean cell length : width > 1.5 : 1.

surface. Of the other members of series *Spicigerae*, *B. ericifolia* differs in having shorter, more strongly revolute and narrower leaves with cuticular papillae, *B. brownii* has pinnately lobed leaves and large cuticular cells of the non-stomatiferous surface, *B. occidentalis* has large, almost isodiametric cuticular cells of the non-stomatiferous surface, *B. littoralis* and *B. seminuda* have larger leaves with only recurved margins, *B. tricuspis* has leaves similar to series *Abietinae*, and *B. verticillata* has elliptic leaves and large nearly isodiametric cuticle cells of the non-stomatiferous surface. The fossils are therefore closely related to *B. spinulosa* but are sufficiently different to warrant separate specific status.

Figure 3.57 : Extant distribution of *Banksia spinulosa*.

Banksia spinulosa grows widely in the coastal and mountain strip of eastern and south-eastern Australia (Figure 3.57), where it occurs in woodlands and heaths of wettish areas. It is animal pollinated (Whelan and Goldingay 1986) and usually serotinous (George 1984).

***Cenarrhenes nitida* (RPU1, RE, ME)**

Specimens examined : ME 615-630
RE 8053-8092
RPU 461, 465

Discussion : The cuticle of this taxon was illustrated by Jordan *et al.* (1991) from the Melaleuca Inlet sediments, and the presence of the fruit in the Regency sediments was recorded by Fitzsimons *et al.* (1990). Leaf fragments with good cuticle and teeth (Figures 3.58 a, c & e & 3.59 a) which occur in the Regatta Point sediments are consistent with *C. nitida* (Figures 3.58 b, d & f & 3.59 b). Cuticle fragments and the woody parts of several drupes of this species occur in the Regency sediments. This taxon is known from the Melaleuca Inlet sediments only from cuticle fragments, which are consistent with extant *C. nitida* and inconsistent with any other extant taxon. Among modern species, the distinctive cuticle with wide, randomly aligned, paracytic stomata with T-pieces, uniformly distributed on one surface (Figure 3.58 d), interspersed with irregularly arranged rectangular cells, and ribbing of the outer surface (Figure 3.58 f) occur only in *C. nitida*. *Cenarrhenes nitida* occurs occasionally in Pleistocene sediments in Tasmania.

Cenarrhenes is a monotypic genus endemic to Tasmania. It occurs mainly as a small tree or tall shrub in rainforest and other wet forest in western, south-western and southern Tasmania, but also occurs in sedgeland/heath. It has conspicuous reddish black fleshy fruits and may be bird dispersed.

***Hakea* species (RPU1, ME)**

Specimens examined : ME 630-632
RPU 502

Discussion : The cuticle of *Hakea* sp. was recorded from the Melaleuca Inlet sediments and was illustrated by Jordan *et al.* (1991). Leaf fragments with cuticle (Figures 3.59 c & e) occur in the Regatta Point sediments consistent with acicular leaved species of *Hakea* (Figure 3.59 d & f). The cuticle is indistinguishable from the cuticle from the Melaleuca Inlet sediments, but cannot be distinguished from many other *Hakea* species.

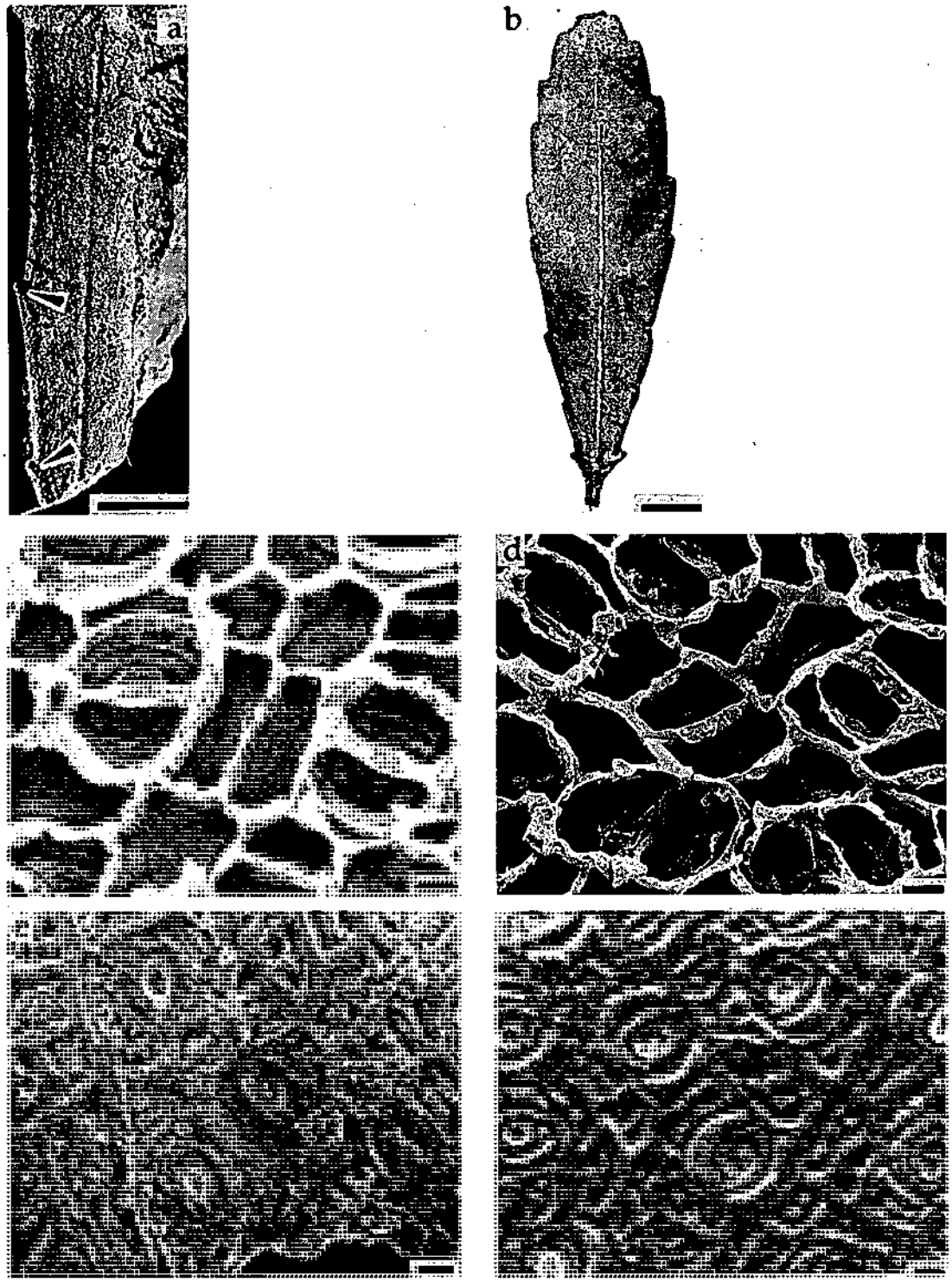


Figure 3.58 : *Cenarrhenes nitida*. a, c & e : Fossil *C. nitida* from Regatta Point. b, d & f : Extant *C. nitida*. a : Impression of leaf fragment. Note the teeth (arrows) and midrib. b : Leaf. c & d : Inner surface of stomatiferous surface. e & f : Outer surface of stomatiferous surface. Note the ribbing and compare it with other Proteaceae, e.g. Figures 3.51 d, 62 f & 66 f. Scale bars for a & b = 5 mm, for c, d, e & f = 10 µm.

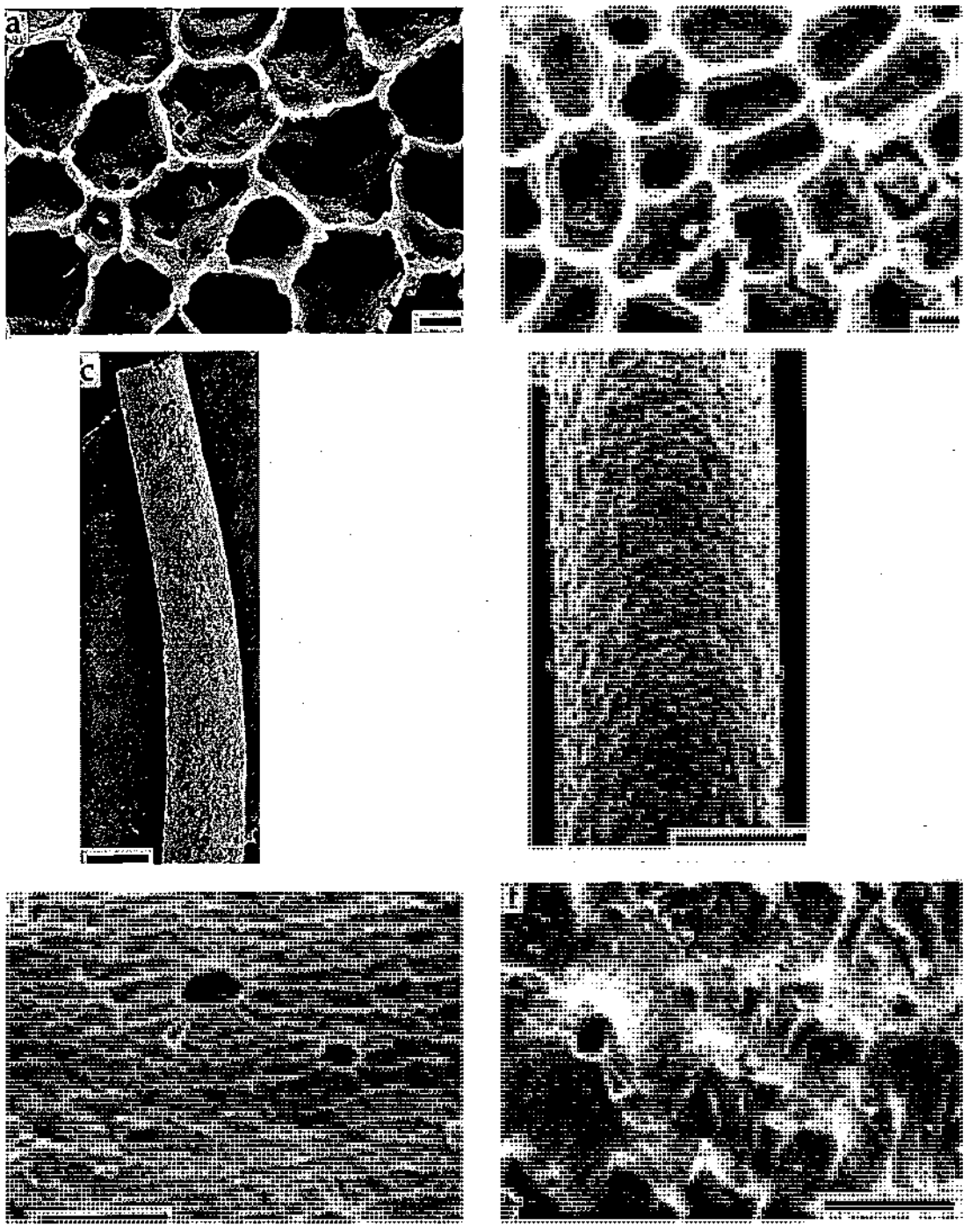


Figure 3.59 : *Cenarrhenes nitida* and *Hakea*. a : Inner surface of cuticle of non-stomatiferous surface of fossil *C. nitida* from Regatta Point. b : Inner surface of cuticle of non-stomatiferous surface of extant *C. nitida*. c & e : Fossil *Hakea* from Regatta Point. d & f : Extant *H. lissosperma*. c & d : Leaf fragments. e & f : Detail showing stomates (arrow) overarched by a cone of about 12 epidermal cells. Scale bars for a & b = 10 µm, for c & d = 0.5 mm, for e & f = 50 µm.

Cuticle with the cones of cells covering the stomata (Figure 3.59 e & f) occur only in *Hakea*. Cuticle fragments in the Melaleuca Inlet sediments have cuticle consistent with many species of this large genus. *Hakea* species are common in many sclerophyllous heath communities. They have woody follicles and heavy winged seeds. These fossils represent the first macrofossil records of *Hakea*.

***Lomatia* aff. *tasmanica* (ME)**

Specimens examined : ME 633-637

Discussion : This fossil taxon was illustrated and its identification justified by Jordan *et al.* (1991). The identification of *Lomatia* cf. *tasmanica* (Figures 3.60 a, c & e) from the Melaleuca Inlet sediments is based on several well preserved but incomplete leaves. The cuticle morphology and leaf shape of the fossils are entirely consistent with extant *L. tasmanica* (Figures 3.60 b, d & f) and some extant forms of *L. tinctoria* R. Br., but is quite distinct from all other extant species. *Lomatia tasmanica* only occurs in a small rainforest patch about 12 km from Melaleuca Inlet (see Figure 1 in Jordan *et al.* 1991 : Appendix 3). *Lomatia tinctoria* occurs widely in central and eastern Tasmania, but is rare in western Tasmania and is apparently absent from soils derived from Cambrian and Precambrian rock types. These rock types make up the geology of the Melaleuca Inlet region (Williams and Corbett 1977). *Lomatia* fossils are known from the Tasmanian Oligocene Cethana sediments (Carpenter and Hill 1988). *Lomatia* species are unlikely to be well dispersed since they have dry fruits and heavy winged seeds.

***Orites revoluta* (RPU1)**

Specimens examined : RPU 472

Discussion : This fossil leaf (Figures 3.61 a, c & e) is indistinguishable in leaf shape and size, and cuticular morphology from extant *Orites revoluta* (Figures 3.61 b, d & f). The small, tightly revolute margined leaves occur in several proteaceous taxa, (e.g. some Western Australian *Banksia* species : see Table 3.1), and other taxa (e.g. the composite *Olearia ledifolia*, with which *Orites revoluta* often grows) but

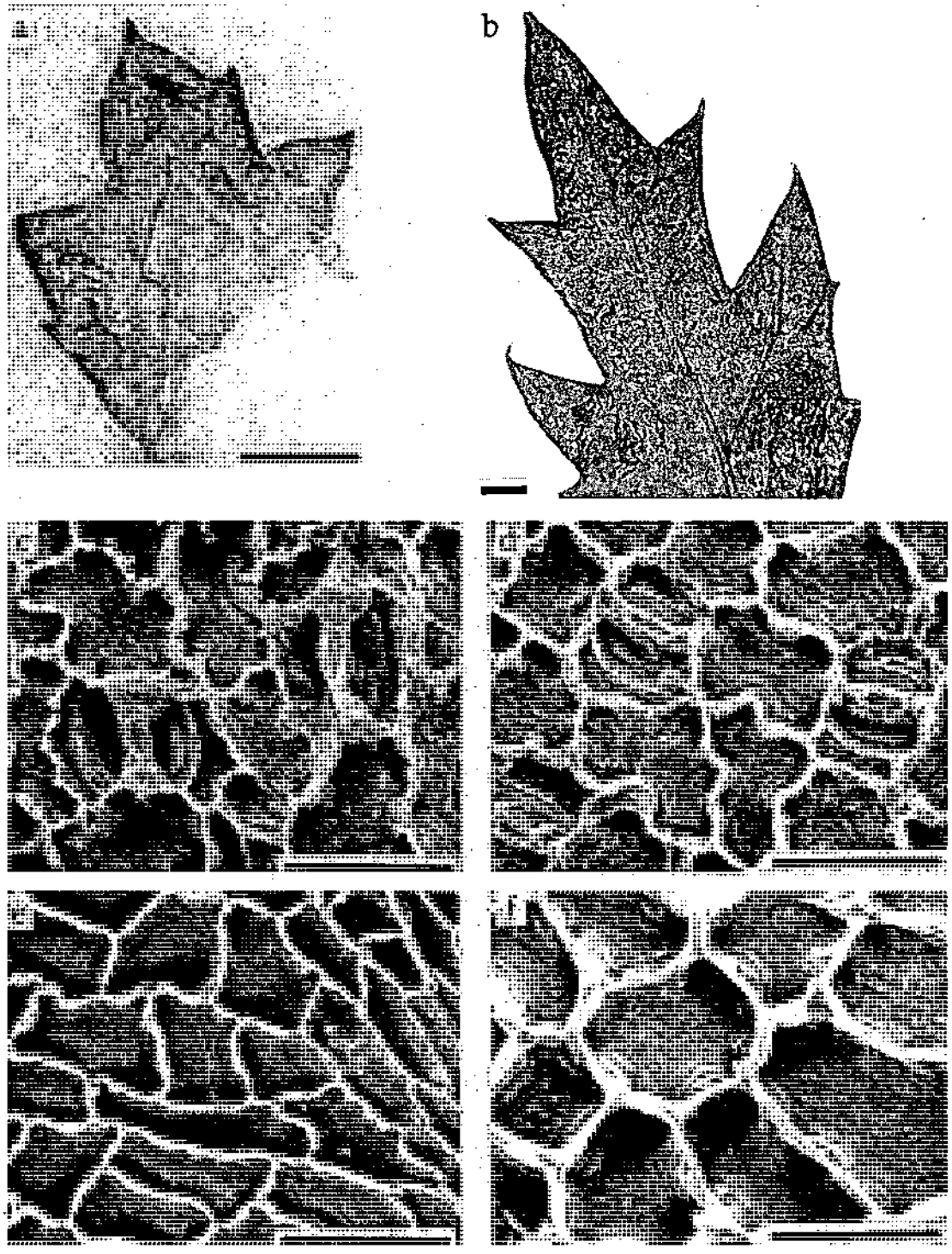


Figure 3.60 : *Lomatia*. a, c & e : Fossil *Lomatia* aff. *tasmanica* from Melaleuca Inlet. b, d & f : Extant *L. tasmanica*. a & b : Leaf fragments. c & d : Inner surface of cuticle of stomatiferous surface. e & f : Inner surface of cuticle of non-stomatiferous surface. Scale bars for a & b = 1 mm, for c, d, e, & f = 50 μm.

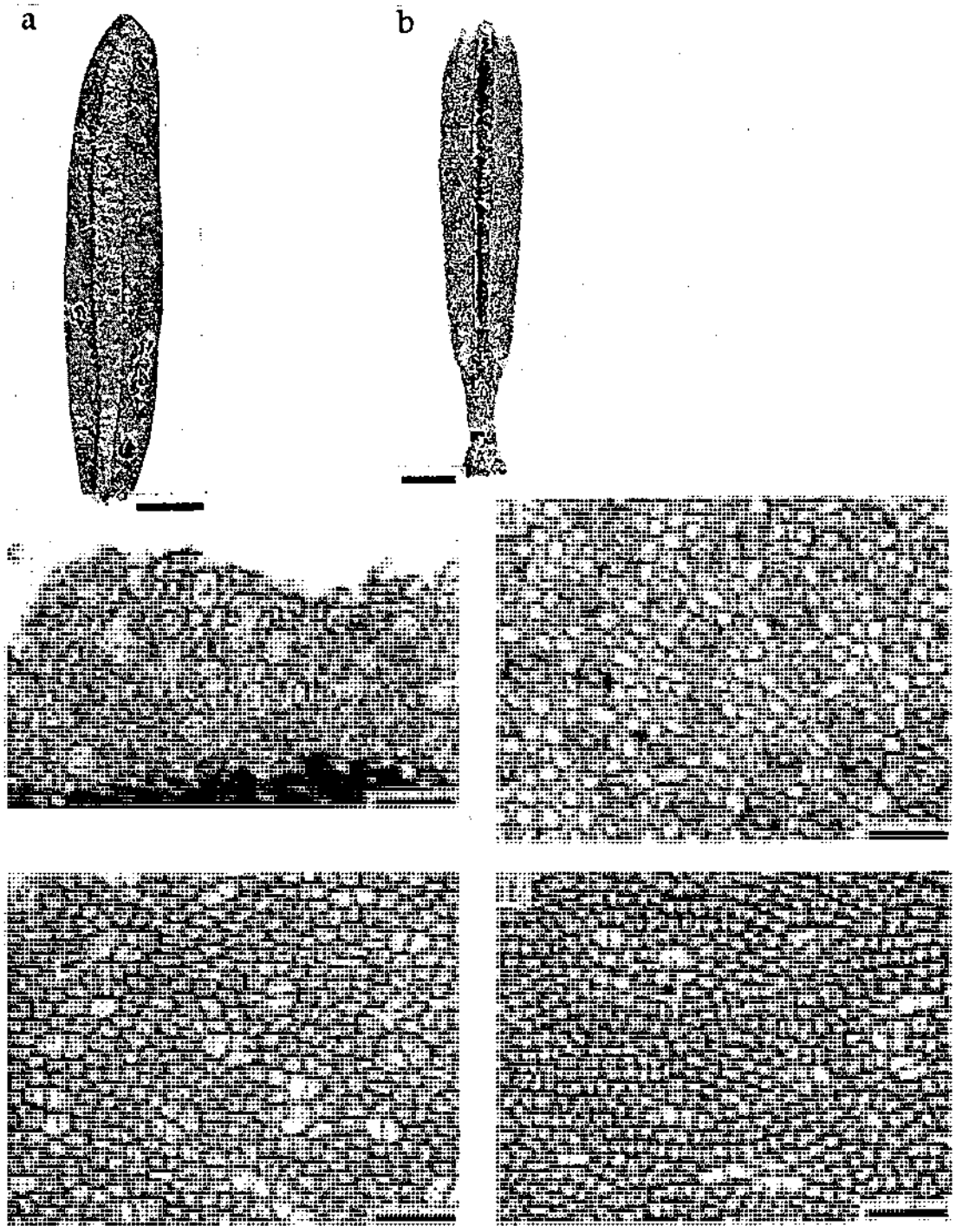


Figure 3.61 : *Orites revoluta*. a, c & e : Fossil *O. revoluta* from Regatta Point. b, d & f : Extant *O. revoluta*. a & b : Leaves. c & d : Cuticles of stomatiferous surface. e & f : Cuticles of non-stomatiferous surface. Note the elliptical trichome bases of enlarged cells (arrows). Scale bars for a & b = 1 mm, for c, d, e & f = 100 μm.

combined with cuticle characters uniquely identify *Orites revoluta*. The cuticle of the non-stomatiferous surface (Figure 3.61 e) has the large multicelled trichome bases which occur in most *Orites* species, and some other members of the Grevilleoideae, but one genus of Proteoideae (*Faurea*) (R. J. Carpenter pers. comm.). The epidermal cells are identical to those of extant *O. revoluta* (Figure 3.61 f). The cuticle of the stomatiferous surface with stomata evenly distributed between the midrib and revolute margin, broadly reniform guard cells, and abundant single celled trichome bases (Figure 3.61 c) are characteristic of *O. revoluta* (Figure 3.61 d). *Orites revoluta* is a common shrub of alpine and sub-alpine areas of Tasmania. There are no macrofossil records of *Orites* prior to this study.

***Orites* sp. nov. (RPU2)**

Specimens examined : RPU 508, 513, 519, 530, 560, 4365-4412

Diagnosis : Leaf base truncate, petiole nearly as long as lamina. Venation craspedodromous. Outer surface of stomatiferous surface covered with large epidermal papillae.

Type Specimen : RPU 560.

Description : Leaves ovate, lamina about 4 cm by 2.5 cm, irregularly toothed, occasionally with secondary teeth, teeth concave on basal side, convex on apical side, sinuses rounded, apex acute to acuminate, base truncate, petiole nearly as long as lamina. Venation with prominent midrib, some strong secondary veins leading irregularly to teeth, weaker secondary veins looping to join both the distal and apical stronger secondary veins, reticulate between secondary veins, with well developed areolation, veinlets branched up to four times. Cuticle of stomatiferous surface with randomly aligned stomata, outer surface covered with epidermal papillae which encrypt stomata, stomata paracytic, with weak T-pieces of cuticle at the stomatal poles, epidermal cells isodiametric, rounded, stomata restricted to areoles between major veins, trichome bases common, large, often elliptical, of 2-10 ± rectangular cells. Cuticle of non-stomatiferous surface of irregularly arranged, ± isodiametric, ± rounded, thick-walled, porose cells, trichome bases common, large, ± elliptical, of (1-) 6-15 darker staining rectangular porose cells.

Discussion : Well preserved leaves (Figure 3.62 a) of a Proteaceous taxon occur in the Regatta Point sediments. It is assigned to *Orites* due to the presence of a combination of characters, epidermal papillae, general cuticle morphology, leaf shape and venation. Each of these characters occurs in other genera, but no other genus has more than one or two of them. The cuticle of this taxon (Figures 3.62 e & 3.63 a & c) differs from that of *Orites diversifolia* (Figures 3.62 f, 3.63 b & d) only in the presence of T-pieces of cuticle at the stomatal poles, which are, however, present in other species of *Orites*. The fossil has compound epidermal papillae, but these occur in other, scarcely related proteaceous genera including *Telopea truncata* (Figure 3.66 e). The multicelled elliptical trichome bases are typical of *Orites* (Figures 3.63 c & d and 3.61 e & f), and do not occur in other genera with compound epidermal papillae, although they occur in other genera of the Grevilleoideae. The stomata, however, have T-pieces which do not occur in *O. diversifolia*, but occur in other species of *Orites*. Other species of *Orites* differ in several cuticle characters, notably in the absence of epidermal papillae, which appears to be derived in *O. diversifolia*, in the size of the epidermal cells and in the shape of the guard cells, which are more curved in species other than *O. diversifolia*.

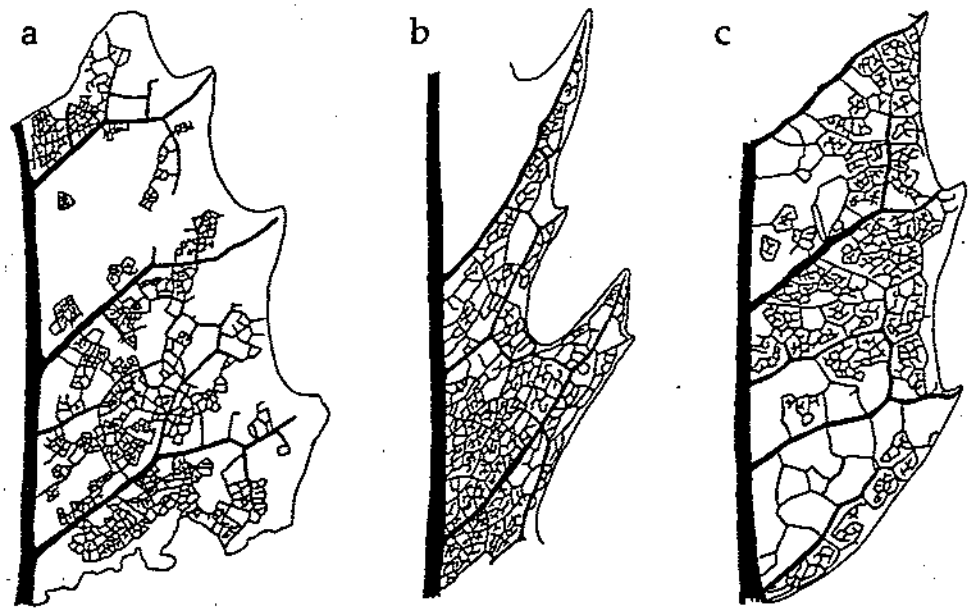


Figure 3.64 a, b & c : Drawings of venation. Note the strong secondary veins leading to the teeth, and the weaker secondary veins looping to join the stronger secondary veins. a : Fossil *Orites* sp. nov. from Regatta Point. b : Extant *O. diversifolia*. c : Extant *O. milliganii*.

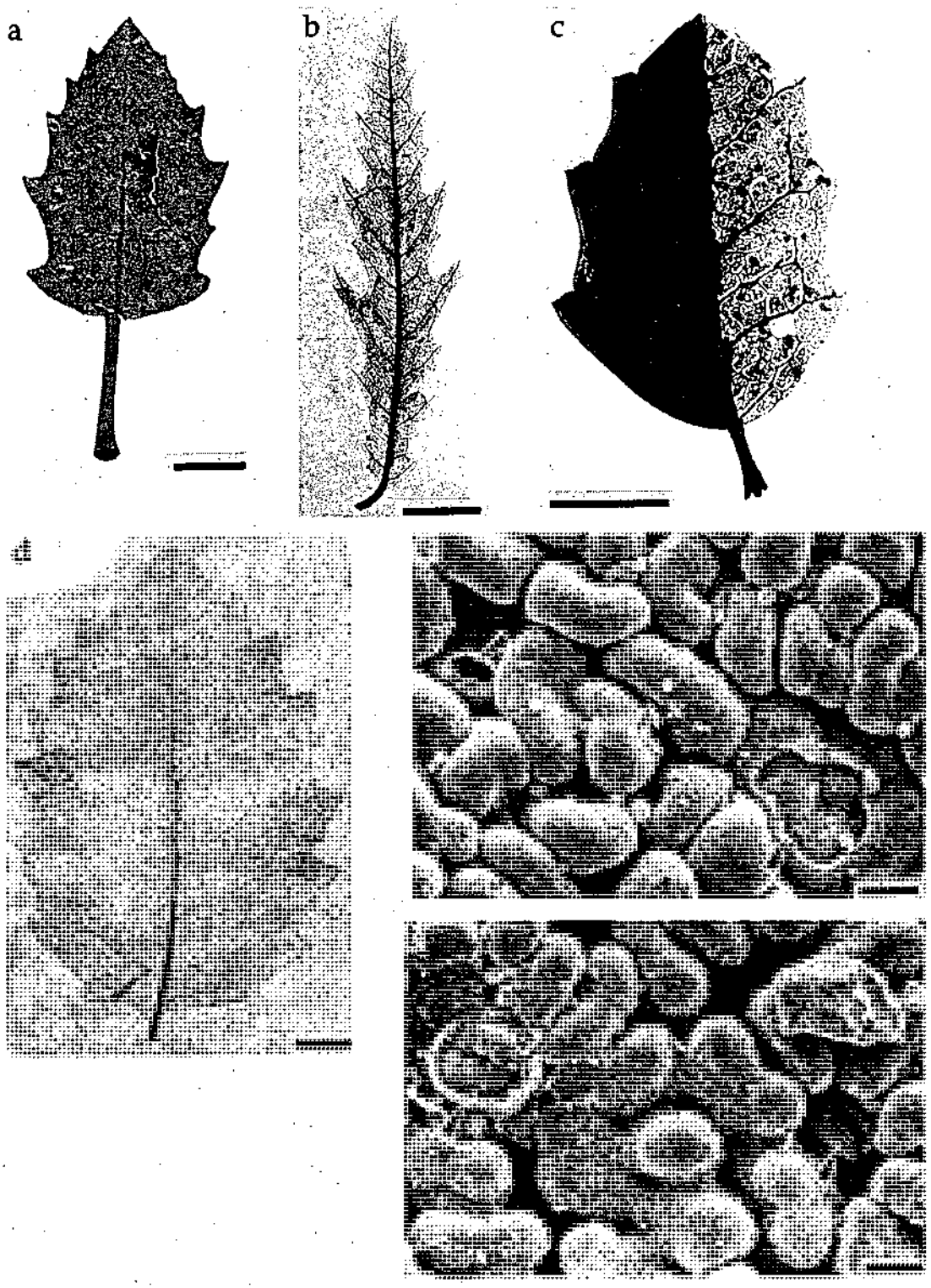


Figure 3.62 : *Orites* and *Lomatia*. a & e : Fossil *Orites* sp. nov. from Regatta Point. b & f : Extant *O. diversifolia*. c : Extant *O. milliganii*. d : Extant *Lomatia arborescens*. a, b, c & d : Leaves. Note the clearly semicraspedodromous venation of *L. arborescens* but similar leaf shape to the fossil. e & f : Outer surfaces of stomatiferous surface showing stomates (arrows), trichome bases (arrows) and papillae. Scale bars for a, b, c & d = 10 mm, for e & f = 10 μm.

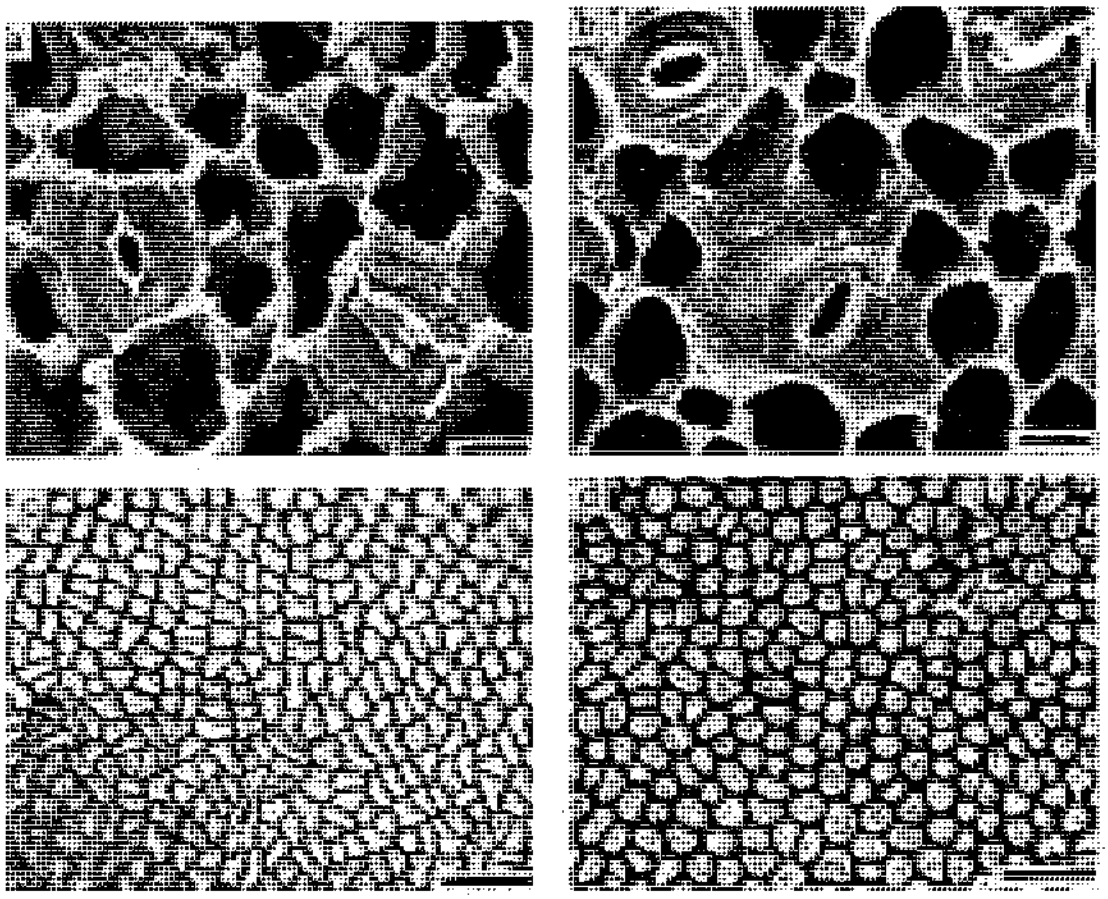


Figure 3.63 : *Orites*. a & c : Fossil *Orites* sp. nov. from Regatta Point. b & d : Extant *Orites diversifolia*. a & b : Inner surfaces of cuticle of stomatiferous surface. Note the deep depressions forming the papillae, indicating that the papillae are extensions of the epidermal cells, not just thickenings of the cuticle. c & d : Cuticle of non-stomatiferous surface. Note the large elliptical trichome bases (arrows). Scale bars for a & b = 10 µm, for c & d = 100 µm.

The leaf morphology of the fossil taxon is clearly outside the range of *O. diversifolia* (Figure 3.62 b) which are more or less lanceolate, have obtuse to attenuate bases and short petioles. *O. milliganii* (Figure 3.62 c) has a shorter petiole, and has smaller leaves than the fossil, but is very similar in leaf shape. The leaf size and shape of the fossil species is also very similar to forms of *Lomatia arborescens* (Figure 3.62 d) and *L. ilicifolia*.

The venation of the fossils (Figure 3.64 a) shows a form which appears to be derived in *Orites* (Figures 3.64 b& c) and its probable sister genus *Neorites*. The generalized form of venation within the Proteaceae appears to be brochidodromous (i.e. with secondary veins never reaching the margin, but looping towards the apex and joining the next secondary vein e.g. *Telopea*, Figure 3.66 b & 3.67) in entire leaves, and semicraspedodromous (essentially brochidodromous, except that major tertiary veins leave the loops of the secondary veins and lead to the teeth e.g. *Lomatia arborescens*, Figure 3.62 d) in toothed leaves. *Orites* species with teeth have venation which is virtually craspedodromous (i.e. the secondary veins lead directly to the teeth) (Figures 3.64 b & c) although there are weaker loops leading to weaker secondary veins which do not reach the margins. The fossil taxon shows this character (Figure 3.64 a). This character does, however, appear to also occur in the scarcely related *Cenarrhenes nitida*, but which differs in many other characters (see Figures 3.58 & 3.59).

The cuticles of all Australian *Lomatia* species differ from those of the fossil and of *Orites* species in not having epidermal papillae. *L. ferruginea* and *L. dentata* from South America have papillae, but these appear to of a different form. Unlike the fossils, and like most other *Lomatia* species these species have cuticles with sinuous cell walls. The similarity in leaf form between the fossil and *Lomatia* species is likely to be convergence.

Orites diversifolia is a species of wet forests in Tasmania from sea level to subalpine areas. *Orites* species are species of wet forest, especially rainforest, and alpine and sub-alpine shrubberies in eastern Australia and South America (Figure 3.65). The fossils are therefore from an extinct species of *Orites*, and, based on the similarity of the cuticle, are probably closely related to *O. diversifolia*. *Orites* species are unlikely to be well

dispersed since they have dry fruits and heavy winged seeds.

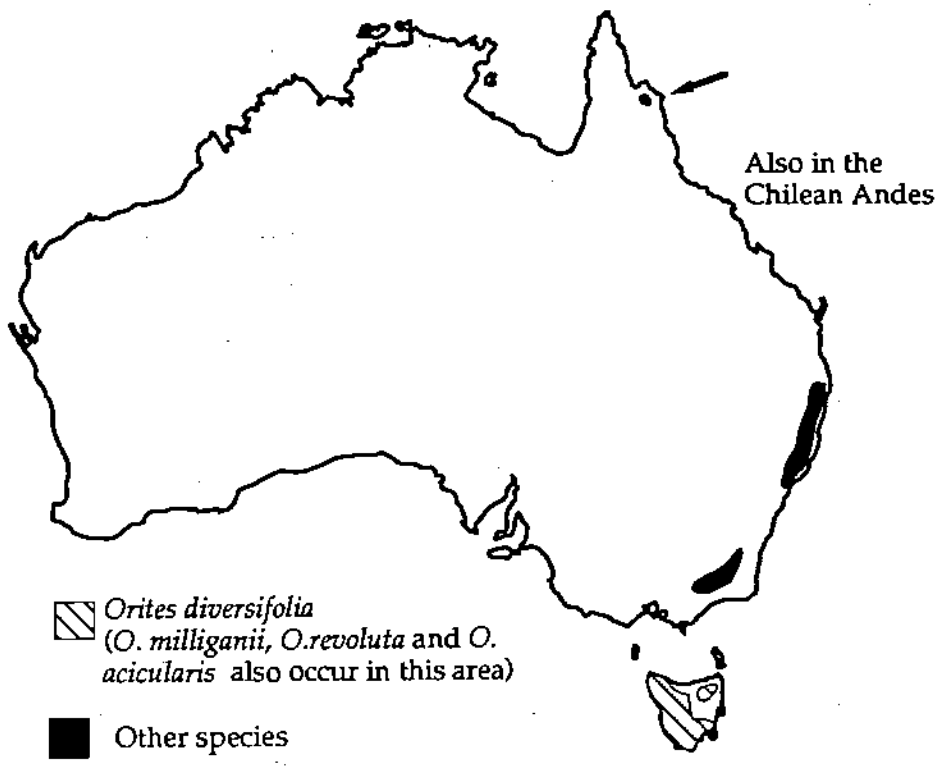


Figure 3.65 : Distribution of extant species of *Orites*.

***Telopea* cf. *mongaensis* (RPU1&2)**

Specimens examined : RPU 319-321, 377-379, 402, 413, 421, 433, 498, 514, 532, 533, 536, 547, 564, 566, 4572-4590, 4593

Description : Leaves entire, linear-lanceolate to lanceolate, shortly petiolate, about 0.5 - 2 cm wide, up to at least 10 cm long, apex acute to obtuse, base slightly attenuate. Venation brochidodromous, midrib not prominent, obscure secondary veins diverging at about 30° from mibrib, scarcely branching. Cuticle of non-stomatiferous surface of more or less isodiametric and rectangular cells with nodulose cell walls. Cuticle of stomatiferous surface with uniformly distributed, randomly aligned stomata, outer surface with toroidal stomata interspersed with short discrete ridges, inner surface with paracytic stomata with prominent T-pieces and broadly semicircular-elliptical guard cells, cells between stomatal complexes similar to cells of non-stomatiferous surface.

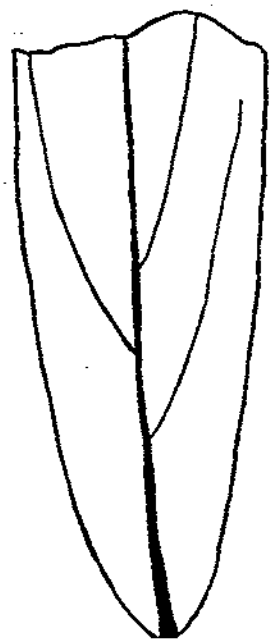


Figure 3. 67 : Drawing of venation of fossil *Telopea* cf. *mongaensis* (RPU 4593).

Discussion : This species (Figures 3.66 a, c & e & 3.67) is described in Hill and Macphail as a species of unknown affinity (RP-079). This species is included in *Telopea* because of the stomata generally aligned with the long axis of the leaf, the isodiametric, regular smooth and thick walled cells of its non-stomatiferous cuticle, its entire margined leaves and its large, round, paracytic stomata with prominent T-pieces (Figure 3.66 c), the outer surface of the cuticle of the stomatiferous surface which is prominently ribbed with compound epidermal papillae (Figure 3.66 e) and the obscure brochidodromous venation with veins diverging from the midrib at angles less than 45° (Figure 3.67). The inner surface of the cuticle of the stomatiferous surface some mainland species of *Telopea* (Figure 3.66 d) share the stomatal morphology and characteristic thickening of the epidermal cell walls with fossil, but *T. truncata* from Tasmania differs in stomatal and epidermal cell form (Figure 3.69 a). The ribs of the external surface are similar to those found in extant species of *Telopea* (Figure 3.66 f) except *T. truncata* (Figure 3.69 b) which has lower surface covered with compound papillae. These ribs are likely to be homologous to the papillae in *T. truncata* and may represent a state derived from the papillae. Compound papillae similar to these occur in several other proteaceous taxa, including the closely related *Embothrium concinnum*, but also the much more distantly related *Orites diversifolia* (see Figure 3.62 f), whereas

the ribs are unique to *Telopea*. Entire leaved *Orites* species have brochidodromous venation, but unlike *Telopea*, have secondary veins arising at high angles from the midrib (most veins diverge from the midrib at angles greater than 45°). The leaf shape and venation are not unlike several species : *T. truncata*, *T. mongaensis* or *T. oreades*, but is dissimilar to *T. speciosissima* or an unnamed species from Gibralter Range, New South Wales which have broader serrate leaves. In particular, the forms with obtuse apices are similar to *T. mongaensis*. The clasping leaf base is unique within *Telopea*. The epidermal cells of the non-stomatiferous surface are also smaller than in any other species of *Telopea*.

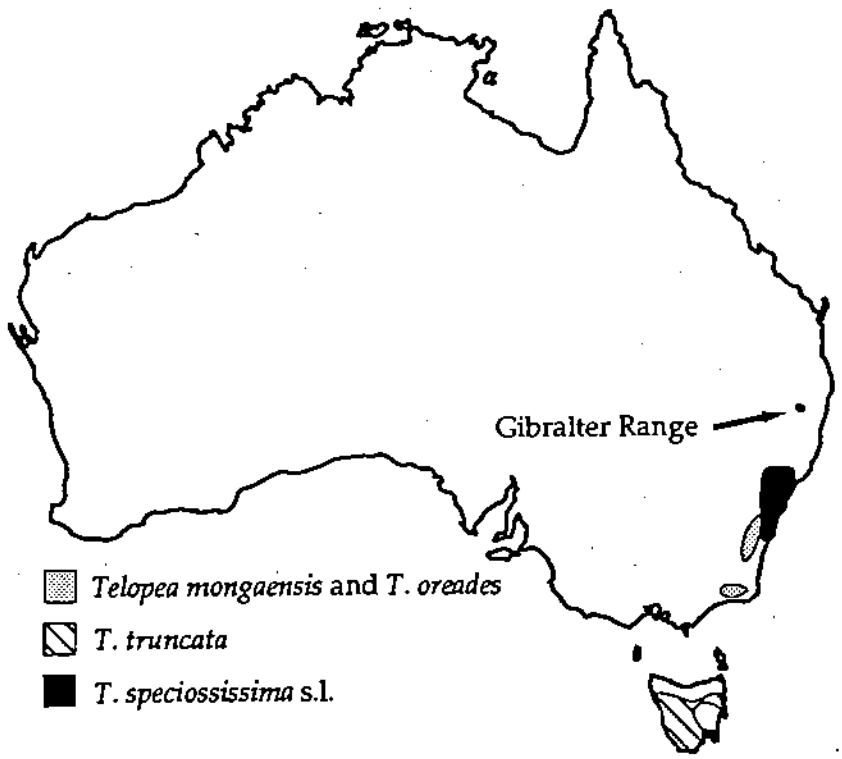


Figure 3. 68 : Distribution of the extant species of *Telopea*.

A wide range of specimens are included in this taxon, including small leaves with clasping petiole bases and obtuse apices, and larger specimens with acute apices. The cuticle morphology is variable also, with differing degrees of development of the ribs of the stomatiferous surface. The degree of tapering of epidermal cell walls of the inner surface of the stomatiferous surface also varies, but this is almost certainly a direct result

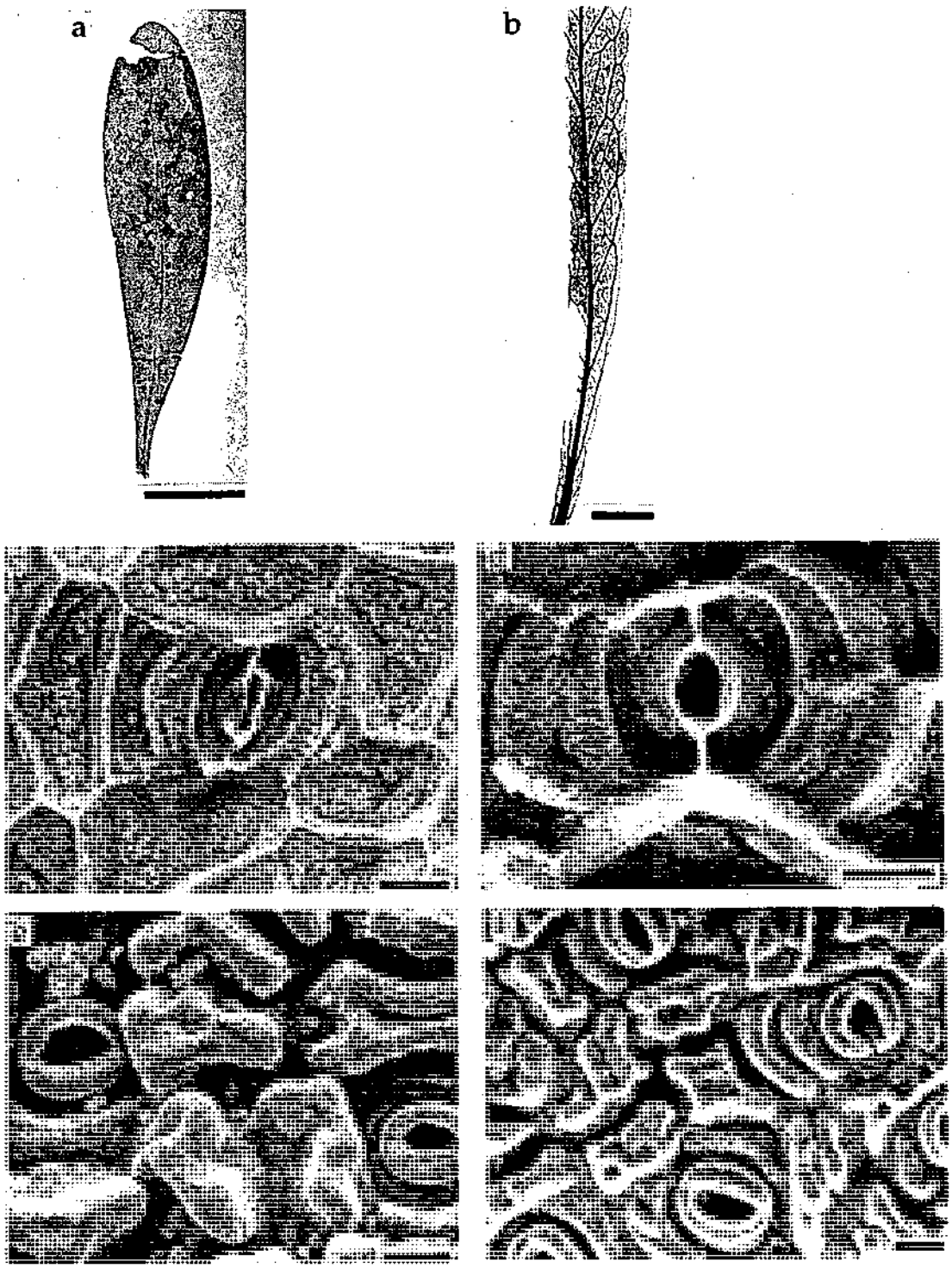


Figure 3.66 : *Telopea* : a, c & e : Fossil *Telopea* cf. *mongaensis* from Regatta Point. b, d & f : Extant *T. mongaensis*. a & b : Leaves. c & d : Inner surface of cuticle of the stomatiferous leaf surface. e & f : Outer surface of stomatiferous leaf surface. Note the large papillae. Scale bars for a & b = 10 mm, for c, d, e & f = 20 µm.

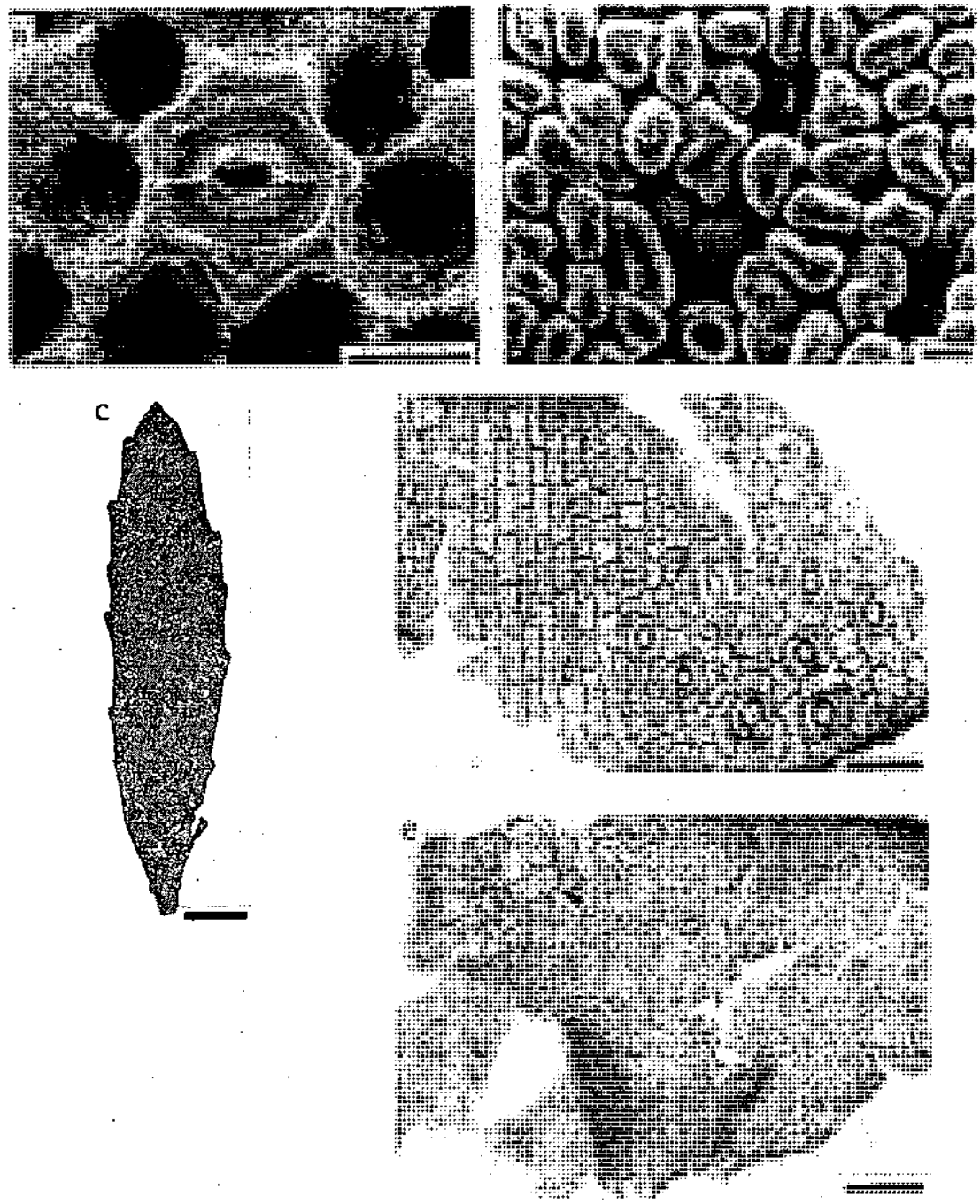


Figure 3.69 : Proteaceae. a & b : Extant *T. truncata*. a : Inner surface of cuticle of the stomatiferous leaf surface. b : Outer surface of stomatiferous leaf surface. c, d & e : Fossil of Proteaceae genus unknown #1. c : Leaf. Note the irregular serration of the leaf. d : Cuticle of the stomatiferous surface. Note the round, paracytic stomata with prominent T-pieces. e : Cuticle of the non-stomatiferous surface. Note the multi-celled trichome-base (arrow). Scale bars for a & b = 20 µm, for c = 2 mm, for d & e = 50 µm.

of differences in the degree of development of the ribs. It is possible that this variation reflects wide natural variation within a species including possibly juvenile and adult forms, or there may be more than one taxon involved here. Extant species of *Telopea* are considerably less variable in cuticle morphology than the fossils, but do show considerable variation in leaf shape and size.

Telopea species are components of cool temperate rainforests, subalpine and other cool moist sclerophyllous woodlands. Figure 3.68 shows the distribution of extant species of *Telopea*. These fossils are from at least one species of *Telopea*, and are not *T. truncata*, the only extant species in Tasmania, although they are not inconsistent with *T. mongaensis* or *T. oreades*. *Telopea* species are unlikely to be well dispersed since they have dry fruits and heavy winged seeds.

Genus unknown #1(RPU1 & 2)

Specimens examined : RPU 534, 572, 4412-4424

Description : Leaves oblanceolate, serrate with rounded teeth, about 1.5 cm long by 0.4 cm broad, apex obtuse. Petiole short. Cuticle of stomatiferous surface with stomata evenly distributed except over midrib, axes of stomata roughly aligned parallel to midrib, stomata paracytic with T-pieces of cuticle at the stomatal poles, epidermal cells sinuous-walled, roughly rectangular. Cuticle of non-stomatiferous surface with epidermal cell isodiametric, more or less hexagonal, granular, trichome bases of about 10 cells.

Discussion : This cuticle of this taxon (Figures 3.69 d & e) has the multiple celled trichome bases and paracytic stomata considered diagnostic of the Proteaceae, and is consistent with the family in all other characteristics. The leaves (Figure 3.69 c) are also similar to many Proteaceous taxa, particularly *Cenarrhenes nitida* (Figure 3.58 b), except that they are considerably smaller. The cuticle differs from both adult and juvenile *Cenarrhenes* (Figure 3.58 d & f & 3.59 b). This species differs from all species of Proteaceae extant in Tasmania, and cannot be readily assigned to any extant Australian genus, and is probably globally extinct.

(?) Proteaceae

Genus unknown #2 (RPU1)

Specimens examined : RPU 558

Description : Leaf/leaflet ovate, about 4 cm broad, more than 5 cm long, base asymmetrical, obtuse. Venation basal acrodromous. Cuticle of non-stomatiferous surface papillose, inner surface with ± rectangular, nearly isodiametric cells, multicelled trichome bases of about 10 cells present. Cuticle of stomatiferous surface papillose, elevated flange of cuticle encrypting each stomate, inner surface with ± rectangular, slightly sinuous epidermal cell walls, stomata randomly oriented, guard cells broadly reniform, T-pieces prominent at the stomatal poles, subsidiary cells lateral, flange of cuticle surrounding subsidiary cells.

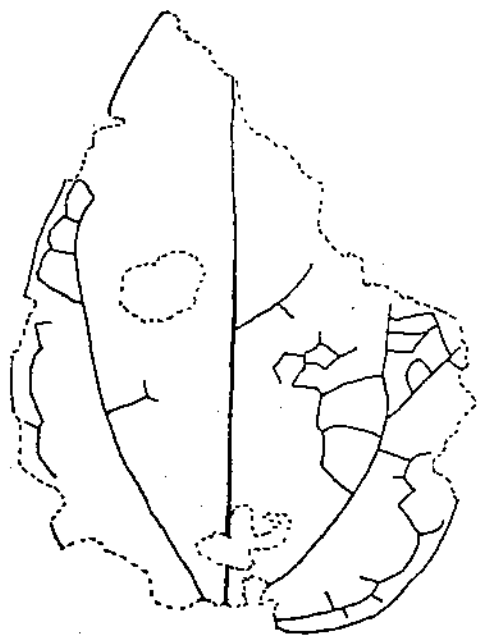


Figure 3.71 : Drawing of venation of (?) Proteaceae genus unknown #2. Note the three veins leading more or less from the leaf base, and the assymetrical leaf shape.

Discussion : This taxon is known from only one leaf fragment (Figure 3.70 a & 3.71). The assymetrical leaf form suggests that this may be a leaflet from a compound leaf. The inclusion of this taxon in the Proteaceae is tentative. The presence of multicelled trichome bases (Figure 3.70 e & f) is usually taken to be diagnostic of the Proteaceae. The stomata, though similar in guard cell morphology to typical Proteaceae stomata, appear to be have about four lateral subsidiary cells (Figure 3.70 c). Extant Proteaceae all appear to have only two lateral subsidiary cells, although

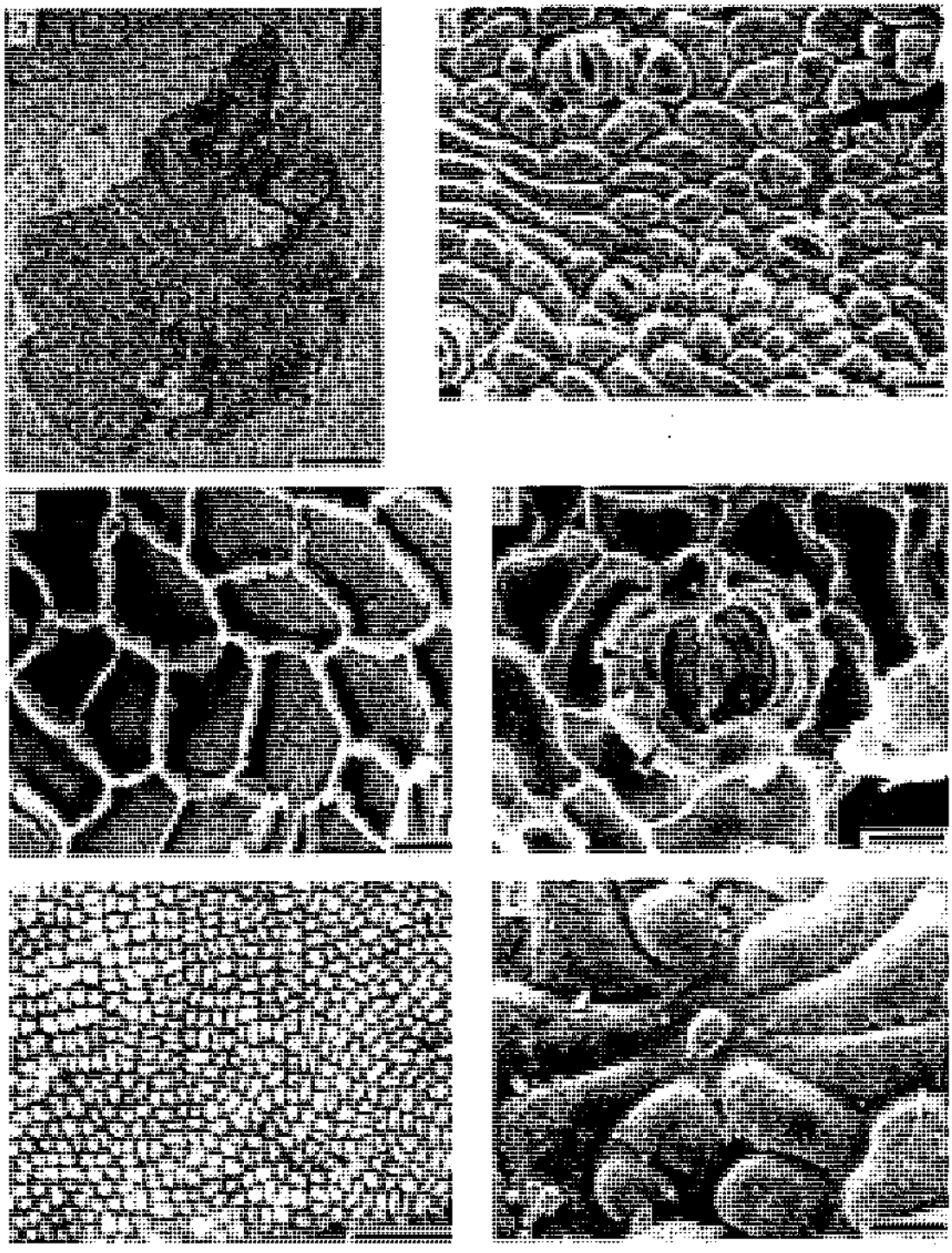


Figure 3.70 : Fossil of (?) Proteaceae genus unknown #2. a : Leaf. b : Outer surface of stomatiferous surface. c : Inner surface of cuticle of non-stomatiferous surface of leaf. d : Inner surface of cuticle of stomatiferous surface showing a stomate. Note that there appear to be about two subsidiary cells (arrows) per guard cell. e : Cuticle of non-stomatiferous surface (transmitted light). Note the multi-celled trichome-base (arrow). f : Outer surface of non-stomatiferous surface showing a multi-celled trichome-base. Scale bars for a = 10 mm, for b, c, d & f = 10 µm, for e = 100 µm.

this is not always clear. Araliaceae have stomata with similar general morphology to the Proteaceae, but which are cyclocytic. The subsidiary cells could be interpreted as reductions from the cyclic state, but trichome bases similar to those of the fossil are not known in the Araliaceae. The subsidiary cells of the fossil may be partitioned, in which case the morphology is consistent with the Proteaceae, and in this case assigning the fossil to the Proteaceae would be justified. However, there is no clear evidence for this, and the taxonomic position of the fossil must remain uncertain. This fossil is clearly extinct from Tasmania because all plant species with leaves of similar size and form have distinctly different cuticle and venation.

Rhamnaceae

***Pomaderris* ? *apetala* (RPU1&2)**

Specimens examined : RPU 212, 234, 574-576

Discussion : These fossils have ovate, bullate leaves with brochidodromous venation with very strong percurrent tertiary veins and crenate margins (Figure 3.77 a) and are within the range of extant *Pomaderris apetala* (Figure 3.77 b). The fossils have brochidodromous venation, and most forms of *P. apetala* have more or less craspedodromous venation. This character, however, is variable in *P. apetala*, with some forms having mixed venation or occasionally brochidodromous venation. Other species of *Pomaderris*, and other genera of Rhamnaceae have brochidodromous venation similar to the fossil, but have entire margins, and weaker venation. No other species extant in Tasmania is similar. *Pomaderris apetala* is a widespread and common small tree of wet sclerophyll forest in Tasmania. No macrofossils of *P. apetala* are known but the pollen is well known from Quaternary sediments.

Rosaceae

***Rubus* cf. *moorei* forma *glabra*(RPU1&2)**

Specimens examined : RPU 206, 346, 440, 456, 4425-4570

Description : Leaves/leaflets bifacial, ovate, irregularly serrate, about 4 cm by 2 cm, apex acuminate, base more or less assymetrically cordate.

Teeth apically and basally acuminate, at 45°-105° from the midrib, first, second and third order teeth present. Venation craspedodromous, some tertiary veins percurrent, tertiary veins leading to teeth mostly distal of parental secondary veins. Thorns present on primary and secondary veins of stomatiferous surface, up to 1.3 mm long on primary veins, shorter on secondary veins, recurved towards the base of the vein. Glabrous apart from occasional trichomes on midrib. Cuticle with sinuous rectangular cells. Stomata doughnut shaped, randomly oriented, distributed evenly on the stomatiferous surface except on primary and secondary veins.

Discussion : This species (Figures 3.72 a & e, 3.73 a & b) is clearly *Rubus* because of the presence of Rosaceae type thorns on the stomatiferous leaf surface, irregularly serrate margins, stomatal morphology and simple craspedodromous venation. The determination of the relationships of this species within *Rubus* is difficult even though the specimens are very well preserved, since *Rubus* is a large, almost worldwide genus, and leaflet morphology is often variable within species and apparently overlapping between species. This taxon shares many characters with *R. moorei* forma *glabra* (Figures 3.72 b & f). This taxon probably deserves species status (Harden and Rodd 1990). Harden and Rodd call this taxon Species A. The fossil taxon also shares several characters with the New Zealand species *R. cissoides* (Figure 3.72 c & 3.73 c & d). The fossil, *R. moorei* forma *glabra* and *R. cissoides* all have cuticle with sinuous cell walls and no trichome bases except occasionally on the midrib of the stomatiferous surface, and only slightly irregular serrations. *Rubus moorei* is hairy on the stomatiferous surface. Unlike the fossils *Rubus moorei* forma *glabra* and *R. cissoides* rarely have thorns occurring on the secondary veins. The thorns of both these species (Figure 3.72 f) are less curved than those of the fossils (Figure 3.72 e). The teeth of *R. moorei* forma *glabra* are straight sided or slightly acuminate and at an angle of about 30° from the midrib with the points curved even further towards the leaf apex, whereas the teeth of the fossils are strongly acuminate and are directed at an angle of about 45° to 105° from the midrib. The teeth of *R. cissoides* are variable but include forms similar to the fossils. The leaf shape in *R. cissoides* is variable, but is always more or less oblong, and differs

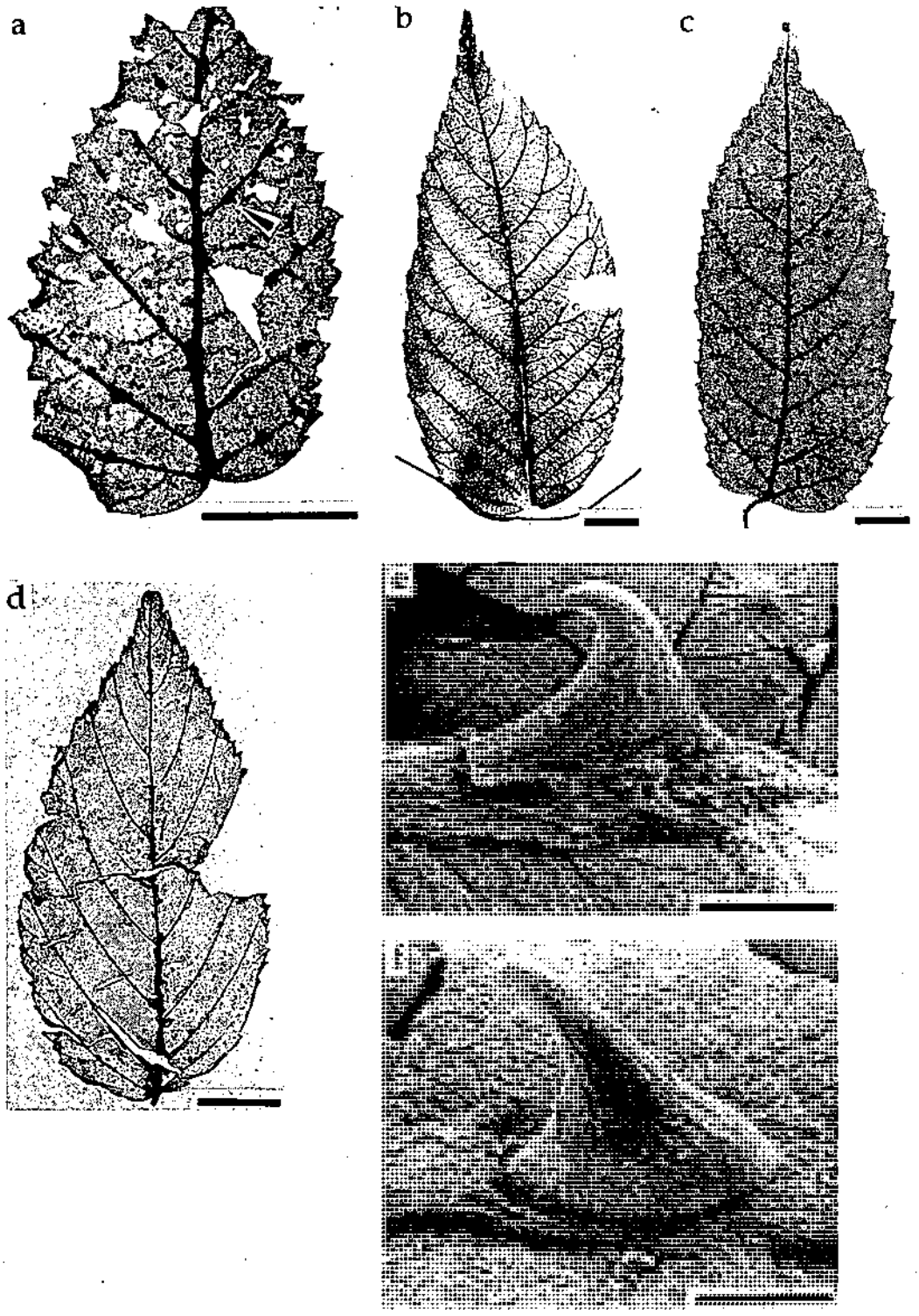


Figure 3.72 : *Rubus*. a & e : Fossil *Rubus* cf. *moorei* forma *glabra* from Regatta Point. b & f : Extant *R. moorei* forma *glabra*. c : *R. cissoides*. d : Extant *R. fraxinifolius*. a, b, c & d : Leaflets. Note the thorns on secondary veins of the fossil (arrow) e & f : Thorns. Scale bars for a, b, c & d = 10 mm, for e & f = 0.5 mm.

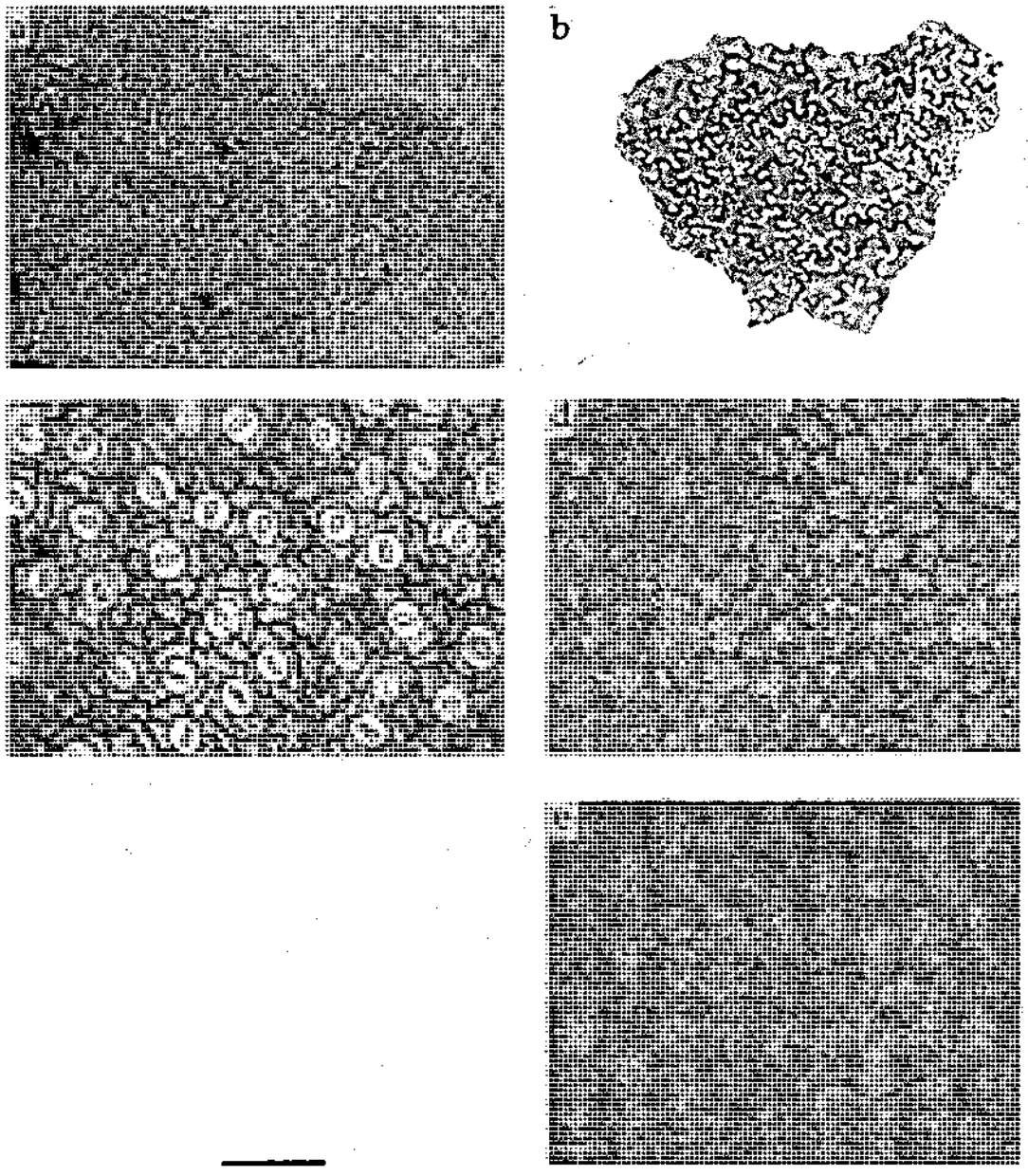


Figure 3.73 : *Rubus* cuticles. a & b : Fossil *Rubus* cf. *moorei* forma *glabra* from Regatta Point. c & d : *R. cissoides*. *R. moorei* forma *glabra* has similar cuticle. e : *R. fraxinifolius*. a & c : Stomatiferous surface. b, d & e : Non-stomatiferous surface. Scale bar = 50 µm for all.

significantly from the fossils which are clearly ovate. *Rubus fraxinifolius* (Figures 3.72 d) is the only other Australian species with only nearly glabrous, slightly irregularly serrate leaflets but differs from the fossils in having few thorns on the leaflets, apically pointed teeth, and non-sinuous epidermal cell walls (Figure 3.73 e). The fossils differ markedly from the extant Tasmanian species *R. gunnianus* which has hairy, smaller, thornless and more dissected leaves, and *R. parvifolius* which is hairy and has more dissected leaves. The presence of mostly assymetrical forms with some symmetrical ones suggest that these leaf-like structures are leaflets of a compound leaves with about 3-7 leaflets. *Rubus moorei* forma *glabra* have palmate leaves with 3-7 leaflets. *Rubus* cf. *moorei* forma *glabra* may therefore have affinities with either *R. cissoides* or *Rubus moorei* forma *glabra*. Species of *Rubus* from elsewhere in the world have some similarities to the fossils. The fossil species, therefore, is clearly extinct from Tasmania, but may belong to an extant *Rubus* species from elsewhere.

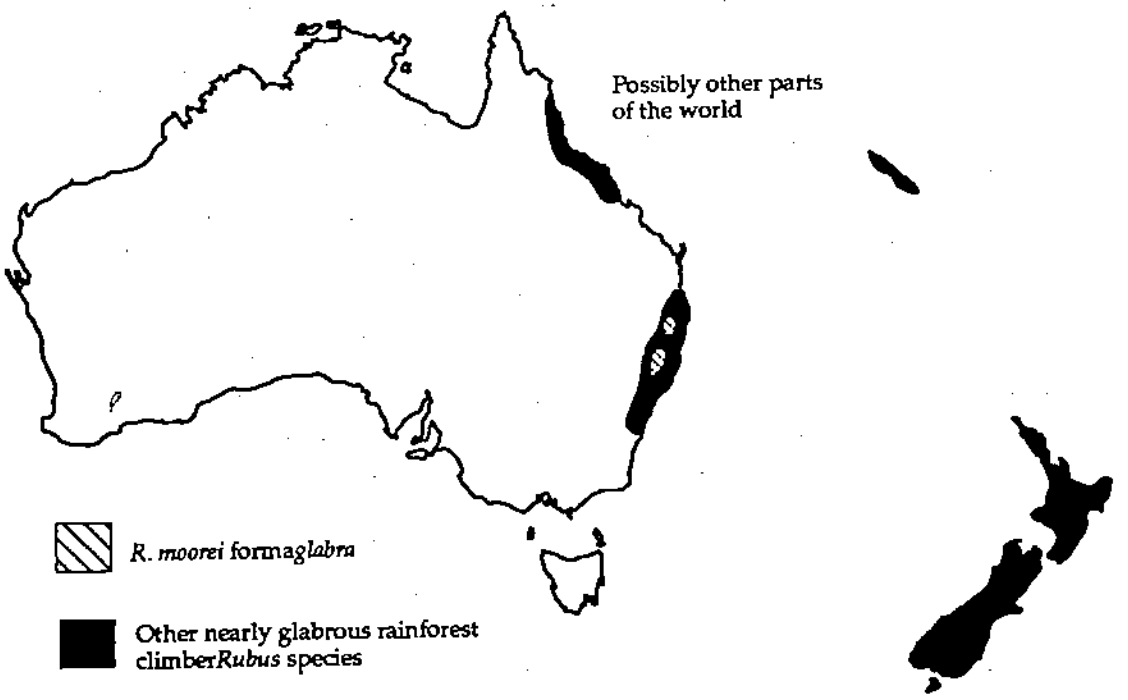


Figure 3.74 : Distribution of nearly glabrous wet forest climber species of *Rubus*.

Rubus moorei forma *glabra* is a climbing shrub in subtropical and

warm temperate rainforest in New South Wales and far southern Queensland (Harden and Rodd 1990; Stanley and Ross 1983). *Rubus cissoides* is a climbing shrub of temperate and subtropical rainforest in New Zealand (Poole and Adams 1986). *Rubus fraxinifolius* is also a climbing shrub and occurs in wet lowland forest of south-eastern Queensland (Stanley and Ross 1983). The fossils share morphological characters with *R. moorei* forma *glabra* and *R. cissoides* which are likely to be of ecological importance and, therefore, it is likely that the fossil species had ecological similarities to *R. moorei* forma *glabra* and *R. cissoides*. *Rubus* cf. *moorei* forma *glabra* was probably a climbing shrub of wet forest. The distributions of *Rubus* species similar to the fossil is illustrated in Figure 3.74.

These fossils are the only macrofossil records of the genus in Australia. *Rubus primaevis* is known as macrofossils from fossil floras in South America (Frengueli 1941) and from the Antarctic Peninsula from the Oligocene/Miocene (Birkenmajer and Zastawniak 1989). *Rubus* species are well adapted to dispersal by birds, with palatable fleshy fruits enclosing hard resistant seeds.

Rutaceae

***Acradenia* sp. (RPU1)**

Specimen examined : RPU 317, 370

Discussion : These fossils have cuticle (Figures 3.75 c & e), prominent glands and leaf size (Figure 3.75 a) indistinguishable from *A. frankliniae* (Figure 3.75 b, d & f)(Figure 3.75 b). However, it has entire margins (Figure 3.76). Extant *Acradenia* species seem to always have serrate margins. This fossil is therefore unlikely to be *A. frankliniae*. *Acradenia frankliniae* is a shrub or tree of wet forest margins and is restricted to a small area in western Tasmania. The cuticle of the other species of *Acradenia*, *A. euodiiformis* (Figure 3.75 g), is scarcely distinguishable from either the fossil or *A. frankliniae*, but other rutaceous taxa have cuticles which are clearly distinct from the fossil. Other species of *Acradenia* are relatively widespread in rainforests of Australia. This taxon is therefore almost certainly a species of *Acradenia* and is likely to be an extinct species.

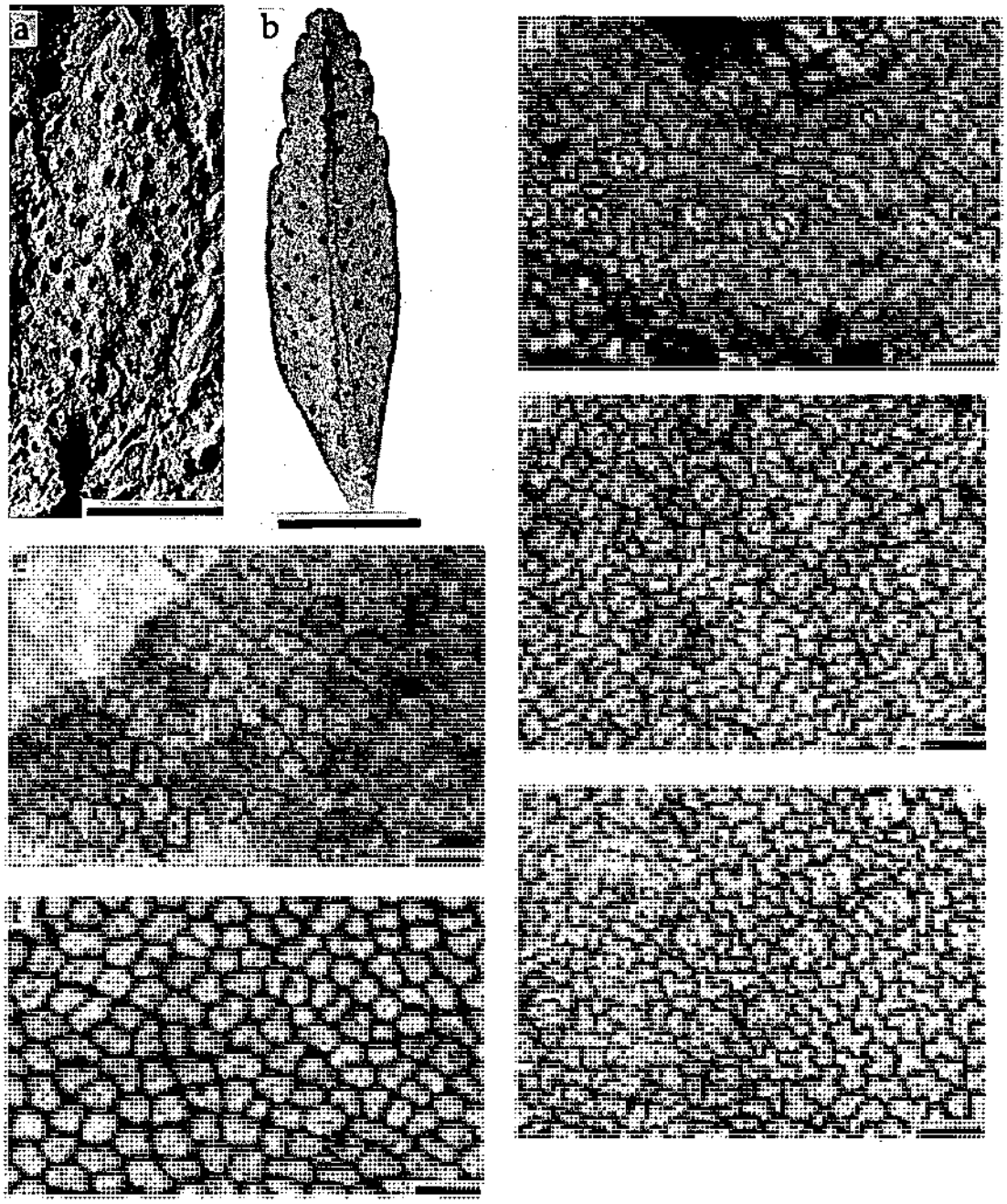


Figure 3.75 : *Acradenia*. a, c & e : Fossil *Acradenia* species from Regatta Point. b, d & f : Extant *A. frankliniae*. g : Extant *A. euodiiformis*. a : Leaflet impression. b : Leaflet. c, d & g: Cuticles of stomatiferous surface. e & f : Cuticles of non-stomatiferous surface. Scale bars for a & b = 5 mm, for c - g = 50 μm.

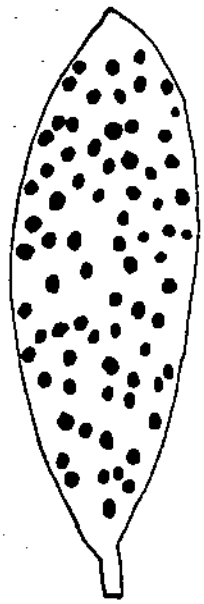


Figure 3.76 : Drawing of leaflet impression of fossil *Acradenia* sp. from Regatta Point. Note the prominent glands and the entire margin.

Winteraceae

Tasmannia ? lanceolata (RPU1)

Specimens examined : RPU 040

Discussion : The seeds (Figure 3.77 d) of *Tasmannia lanceolata* are highly distinctive in the Tasmanian flora. Seeds consistent with them occur in the Regatta Point sediments (Figure 3.77 c) (Hill and Macphail 1985). The fossils may, however, be one of the numerous other species of *Tasmannia* from elsewhere. *Tasmannia lanceolata* is a tree or shrub in wet forest, sub-alpine and alpine areas in Tasmania. Other species of *Tasmannia* occur in similar habitats including sub-tropical forest on mainland Australia, some of these may prove to be conspecific with *T. lanceolata*. *Tasmannia lanceolata* seeds are well dispersed by birds and are common rainforest early successional plants (Read and Hill 1983).

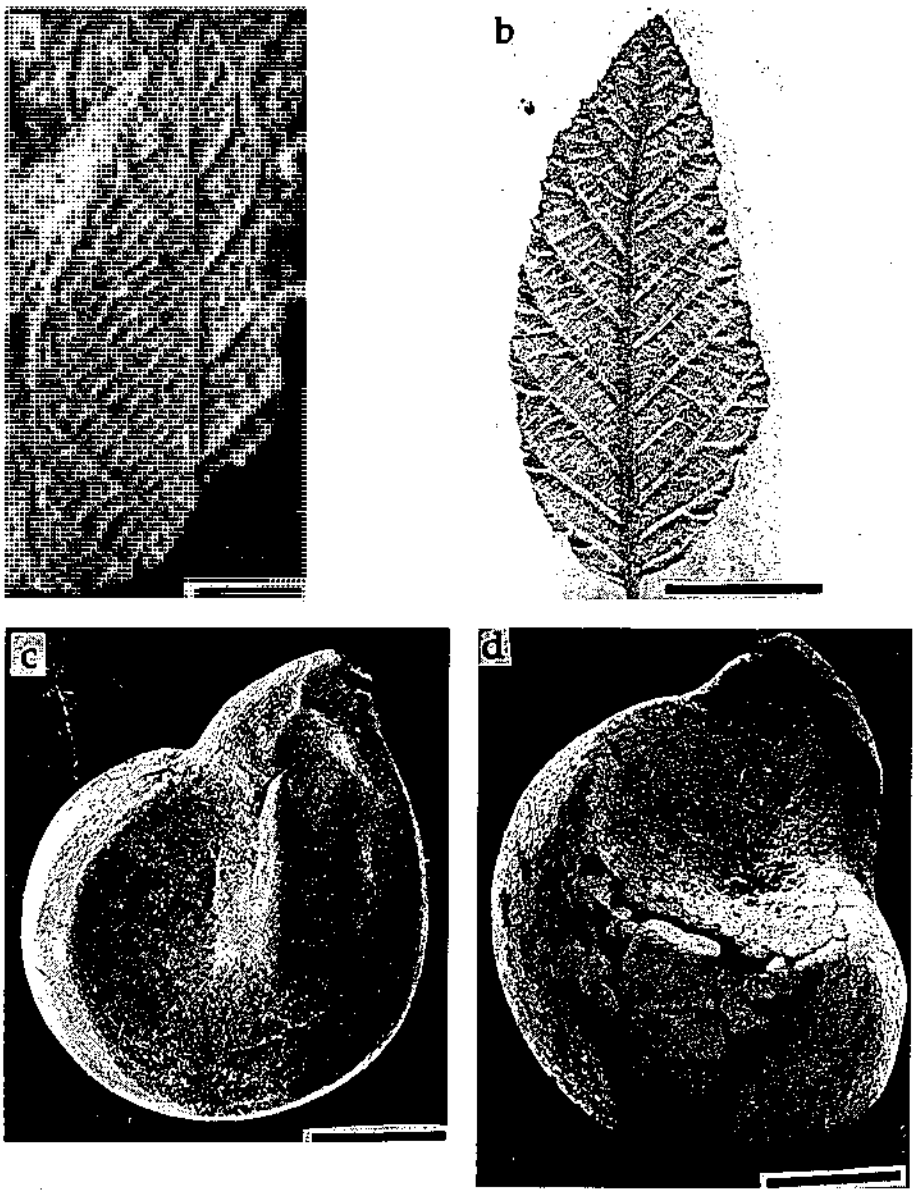


Figure 3.77 : *Pomaderris* and *Tasmannia*. a : Fossil leaf of *Pomaderris* ? *apetala* from Regatta Point. b : Extant leaf of *P. apetala*. The dense covering of stellate trichomes on this leaf surface exaggerate the thickness of the veins. c : Fossil seed of *T.* ? *lanceolata* from Regatta Point. d : Extant seed of *T. lanceolata*. Scale bars for a & b = 10 mm, for c & d = 0.5 mm.

Chapter 4 : Floristic Taphonomy and Reconstruction of Vegetation and Climates

4.1 : Introduction

A brief summary of the Pleistocene vegetation record of Tasmania is given in Chapter 2.

The reconstruction of past vegetation from macrofossils requires caution since the processes of fossilization ensure that fossil assemblages only roughly reflect the local vegetation at the time of deposition. Differences will be both qualitative and quantitative. Factors favouring fossilization of one taxon over another were discussed by Birks and Birks (1980), Ferguson (1985), Hill and Gibson (1986 a) and Carpenter and Horwitz (1988) and include the type of leaf form, the degree of sclerophylly, the content of secondary substances and the buoyancy of the plant part. The type and degree of transport of prospective fossils from vegetation to sediment will also affect which taxa are fossilized (Spicer and Wolfe 1987). Some taxa are highly unlikely to fossilize in moderately high energy systems due to their habit (e.g. ground covering herbs), or due to their structure (e.g. those with fragile leaves, or leaves which are quickly attacked by insects or fungi after abscission) (e.g. Carpenter and Horwitz 1988). Hence, the interpretation of fossil assemblages must be made carefully taking into account these taphonomic biases. In particular, since each deposit has different, partly unknown taphonomic biases it is necessary to be conservative in interpretation of any quantitative data.

Two studies have compared the leaf composition of recent aquatic sediments with local extant vegetation in Tasmania. Such comparisons can be used to infer the relative likelihood of fossilization of different taxa, and in turn are important for interpreting the make-up of the macrofossil assemblage. Hill and Gibson (1986 a) made an extensive study of the species composition of leaf deposits from the bottom of a subalpine lake. Carpenter and Horwitz (1988) made a study of the composition of litter from two stream floors in lowland mixed forest, i.e. forest dominated by eucalypts, but with a predominantly rainforest understorey. Comparisons with the local vegetation was made with informal surveys in both of these studies.

This chapter includes two taphonomic studies (one from Jordan *et al.* 1991, and one new), and reconstructs aspects of the local environment at the time ~~at the time~~ of deposition of the Regatta Point, Regency and Melaleuca Inlet sediments, in the light of these, and previous, taphonomic studies.

4.2 : Materials and Methods

4.2.1 : Fossil Sites

Reconstructions of climate and source vegetation are made for time and places of deposition of the Regatta Point, Regency and Melaleuca Inlet sediments based on the floristics of the macro- and microfossils in the sediments. Vegetation reconstructions have been previously made for all three sites (Hill and Macphail 1985, Fitzsimons *et al.* 1990 and Jordan *et al.* 1991 respectively). The studies here have yielded considerably more information about the Regatta Point sediments than shown by Hill and Macphail so new reconstructions are required. The reconstructions presented by Fitzsimons *et al.* for Regency are modified here. The reconstructions of the Melaleuca Inlet deposit are essentially those presented by Jordan *et al.*

Where a fossil taxon is attributed to an extant taxon it is assumed that the fossil is ecologically similar to the extant taxon, except where some incongruences suggest that this is unlikely. The strength of an ecological inference taken from the presence of a fossil is therefore dependent on the degree of uncertainty in the identification. Incongruences are relatively common, and the strength of a vegetation or climatic reconstruction depends on the number of features supporting each aspect of the reconstruction (e.g. making a climatic inference on the presence of a single taxon is very weak). Morphological similarity between fossil and extant taxa can provide further ecological evidence (e.g. the presence of drip tips is evidence of warm moist conditions (Ellenberg 1985)).

4.2.2 : Taphonomic Analysis

Samples from Hastings Pool, Melaleuca Creek and the Old River sites were used for taphonomic analysis of the floristics of sediments. These sites

and sample collection methods are described in Chapter 2. The Hastings Pool represents a rainforest lake with little transport of the incoming material. The Melaleuca Creek site is a river through mainly scrub vegetation. The Old River site is similar to Melaleuca Creek, except that there was input from distant rainforest.

Each sample was subdivided evenly. More than 1900 identifiable macroscopic remains were counted from random sub-samples of the litter from each of the Old River and Melaleuca Creek sites. More than 250 identifiable macroscopic remains were counted from random sub-samples of each sample in the Hastings Pool sediments.

4.3 : Results

4.3.1 : Taphonomic Analysis

4.3.1.1 : Hastings Pool

Figure 4.1 shows the proportions of each taxon in the samples from the sediments at Hastings Pool, and litter from the surrounding forest.

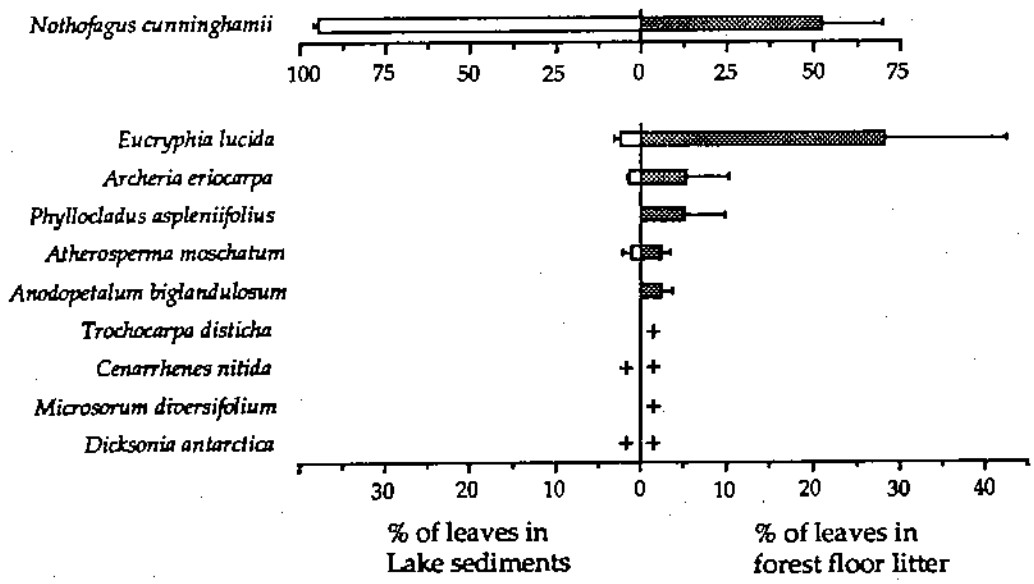


Figure 4.1 : Percentages of leaves of different species found in litter samples derived from the bottom of Hastings Pool (left side) and from the forest floor nearby (right side). The lengths of the bars are mean percentages and the error bars are standard errors. Note that there are two scales (one for *N. cunninghamii*, and the other for the other species). Note that the forest floor samples are more variable and have more species.+ indicates <1%.

The lake sediment samples show lower variation and are fairly homogeneous in relative species abundances, with very little reflection of the make-up of the overhanging and nearby canopy. In contrast the forest floor litter samples show very marked differences in relative species abundances, and their composition reflected the canopy above the sample relatively well.

Nothofagus cunninghamii leaves make up the vast bulk of the identifiable plant organs from the lake bottom sediments, even though this species is not dominant in the immediate vegetation. It also makes up a much higher proportion in the sediments than in the litter samples. It is therefore highly over-represented. Other common species in the nearby forest (*Atherosperma moschatum*, *Eucryphia lucida*, *Anodopetalum biglandulosum*, *Archeria* sp., *Dicksonia antarctica* and *Cenarrhenes nitida*) are all under-represented or absent in the lake sediments. In particular, *Atherosperma moschatum* and *Anodopetalum biglandulosum* are co-dominant in the canopy over the lake but make up only 1% and 0% of the samples, and are therefore highly under-represented or absent in the sediments. *Eucryphia lucida* leaves are rare in the sediments but are well represented in the forest floor samples near *E. lucida* trees and are therefore under-represented in the sediments by comparison to *N. cunninghamii*.

4.3.1.2 : Old River and Melaleuca Creek

Figure 4.2 shows relative proportions of the major species occurring in litter from the Old River and Melaleuca Creek sites. Major differences between the representation of species in the litter and in surrounding vegetation are apparent.

Eucalyptus nitida, *Allocasuarina zephyrea*, *Gleichenia dicarpa*, the sedge families Restionaceae and Cyperaceae and other herbs are all prominent in the vegetation around and upstream of the two litter collection sites, but are rare or absent in the litter and are thus under-represented. This is probably because their leaves are poorly dispersed and/or are apparently susceptible to rapid biological breakdown. The under -representation of *Allocasuarina zephyrea* is explained by the fact that

although these shrubs have robust foliage and are quite common in the surrounding vegetation, they rarely occur along streams. Members of Restionaceae and Cyperaceae are very abundant in all vegetation types in the region except rainforest, but organs of these families were not recognised in the litter samples. These taxa and *Gleichenia dicarpa* exhibit a low growing habit in the region and have quite wiry or rigid foliage which is unlikely to become detached. Also, the cuticle of these plants is usually fragile.

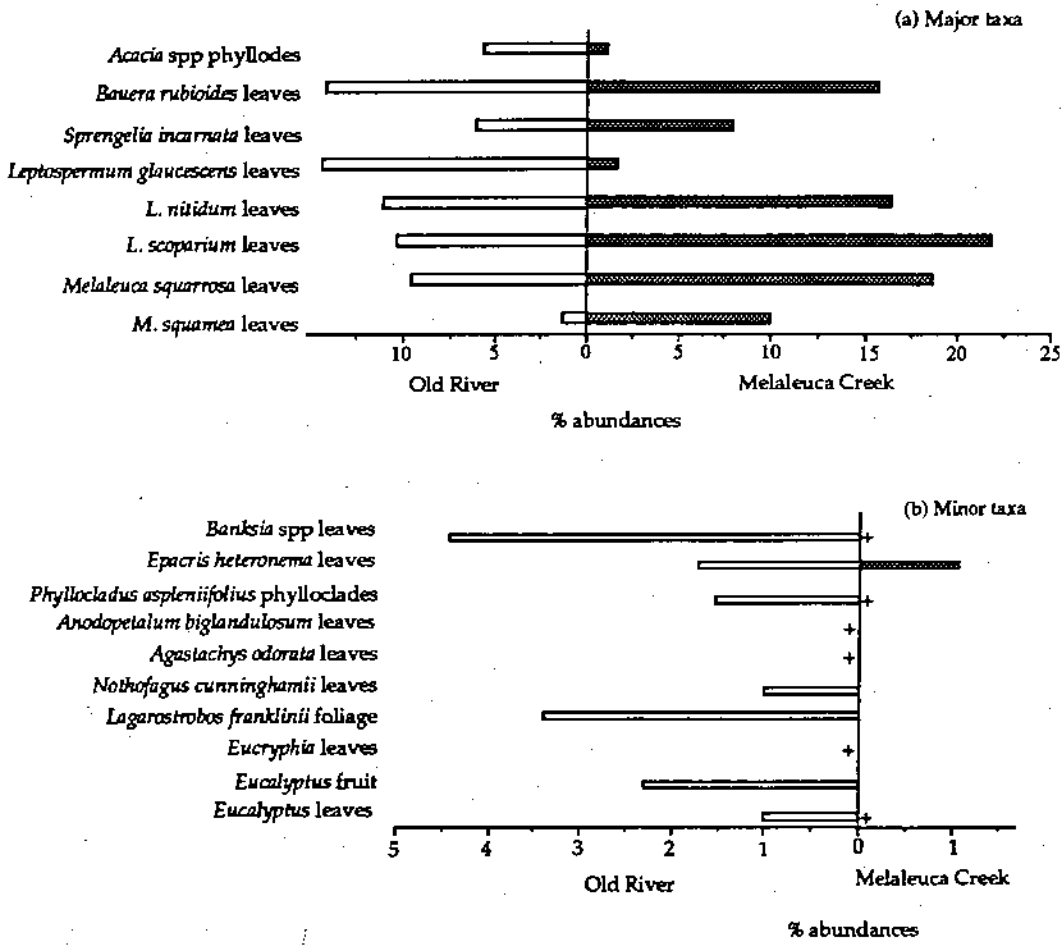


Figure 4.2 : Percentage of identified organs found in water carried litter samples found on the banks of the Old River (left side) and Melaleuca Creek (right side). Note that there are ~~there are~~ two scales. Note that the Old River sample contains small but significant numbers of organs from *Lagarostrobos franklinii*, *Nothofagus cunninghamii*, *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum*.A few taxa which occurred in trace levels have not been included in this graph.+ indicates <1%.

Nothofagus cunninghamii, Lagarostrobos franklinii, Eucryphia lucida and *Phyllocladus asplenifolius* each make up between 0.9% and 3.5% of the Old River sample but are locally rare or absent and are therefore considered to be over-represented in this sample. The nearest source of *N. cunninghamii* and *E. lucida*, and the nearest site where *L. franklinii* and *P. asplenifolius* are common, is a small rainforest patch about 2 km upstream of the collection site. *Phyllocladus asplenifolius* is also over-represented in the Melaleuca Creek litter. Although it makes up only about 0.8% of the litter sample it does not occur for at least 1 km upstream. Phylloclades would therefore be expected to be very rare or absent from the litter, given non-preferential deposition.

Some non-rainforest taxa are well represented in the litter. *Bauera rubioides, Epacris heteronema, Sprengelia incarnata*, three species of *Leptospermum* and two of *Melaleuca* are all common in the local vegetation, but make up very high proportions of the litter (Figure 4.2) and are probably over-represented. These species have small sclerophyllous leaves and with the exception of the *Melaleuca* species, which have particularly fragile cuticle, all seem likely to have a high potential for fossilization.

Reproductive structures are poorly represented, in spite of many being robust and woody, and hence apparently good candidates for preservation. Reproductive structures may be under-represented in the litter because the samples were taken in summer and the sites are certain to have been flushed by winter and spring flooding.

4.3.1.3 : Taphonomic Processes in Tasmania

The leaves in the Old River, Melaleuca Inlet and Hastings Pool samples, and the samples of Hill and Gibson (1986a) and Carpenter and Horwitz (1988) are virtually all from trees and shrubs which grow along the banks of the source streamways. Virtually all herbs in Tasmanian vegetation have foliage which is less robust than the leaves of many Tasmanian woody plants, few shed their leaves as whole structures, as woody plants tend to, and most herbs have low growth habits. Leaves from plants along a waterway are more likely to enter the waterway than leaves

from plants distant from the waterway. The greater the height of a plant not directly overhanging the waterway the more likely its leaves are to enter the waterway. Trees and to lesser extent shrubs, which are along the banks of the river for a moderate distance upstream are, therefore, the most likely source of leaves for fossilization in riverine fossil deposits. In lacustrine deposits the sources will be similar plants from the lake shore and the banks of any inflow stream. Several types of riparian vegetation may contribute to a single deposit (e.g. the contribution of the rainforest patch to the otherwise scrub and sedgeland/heath dominated Old River sample).

There are several indications that some rainforest taxa are strongly represented in modern sediments. Hill and Gibson (1986a) showed that *N. cunninghamii* was over-represented in litter on the floor of a small subalpine lake and Carpenter and Horwitz (1988) suggested that *N. cunninghamii*, *P. aspleniifolius* and *E. lucida* are all likely to be over -represented in fossil assemblages because of their general abundance along water courses, their tree habit and their possession of robust foliage. Similarly, shoots of *Lagarostrobos franklinii* are generally common in riverine litter for a substantial distance downstream of even a small source (personal observation). The composition of the Hastings Pool and Old River sediments also support the idea that these taxa are likely to over -represented in sediments. Therefore, it is likely that all of these species will be fossilized preferentially over most other common taxa extant in Tasmania.

Other rainforest taxa appear unlikely to become fossilized. In particular, *Atherosperma moschatum*, *Anopterus glandulosus* and *Anodopetalum biglandulosum* appear to be poor candidates for fossilization, from the Hastings Pool and Old River evidence, and the results of Carpenter and Horwitz (1988).

The relative absence of *Allocasuarina* in the Old River and Melaleuca sediments, and drift samples from elsewhere in Tasmania suggest that *Allocasuarina* is not at present likely to be fossilized. However, this is more likely to be the result of its modern ecology. The foliage is robust, and well preserved fossils are well known. It is reasonable to assume that if *Allocasuarina* were riparian, and/or a canopy dominant it

would readily enter sediments and fossilize.

Leaves of the small leaved Leptospermoideae (including *Baeckea*, *Melaleuca* and *Leptospermum*) are well represented in the Old River and Melaleuca Inlet samples but are poorly represented in Hill and Gibson's (1986 a) Lake Dobson samples, even though they are very common in the local vegetation. *Eucalyptus* spp. (also Leptospermoideae) are apparently under-represented in all of the samples except Hastings (where *Eucalyptus* did not contribute). The cuticles of these taxa are difficult to prepare by the normal oxidization processes, and these taxa are likely to be poorly represented on fossil sediments partly because the cuticles are prone to degradation, partly because they sink rapidly and partly because they are favoured by invertebrate detritivores. The poor macrofossil record of these taxa does not necessarily indicate their absence, or rarity in the past.

Similarly, many Epacridaceae produce abundant and robust leaves but these have thin and fragile cuticle. If it is sufficiently well preserved the cuticle of most tribes is readily identified but within tribes and there can be great similarity of cuticle and leaf morphology, so identification of species and even genera may be difficult (see chapter 2). Relatively few of the numerous epacridaceous taxa from surrounding Lake Dobson were found by Hill and Gibson (1986 a), but one species (*E. heteronema*) was the most abundant leaf type in the sediments. Leaves of the Epacridaceae are relatively likely to occur in fossil deposits but few taxa are likely to be recognized.

The ease of identification of leaves also affects the contribution they can make to vegetation reconstructions. The modern Tasmanian flora has many taxa with small, entire, sclerophyllous leaves. The leaves of many of these are superficially similar, in spite of being from a wide range of habitats (e.g. lowland rainforest, alpine areas and lowland heath). If the cuticles of these taxa are not distinctive, or if they are poorly preserved, then these taxa are likely to go unrecognized in fossil deposits.

4.3.2 : Macrofossil Composition of the Fossil Sites

4.3.2.1 : Regatta Point (RPU1&2)

Figure 4.3 shows the proportions of macrofossils in RPU1 and each of

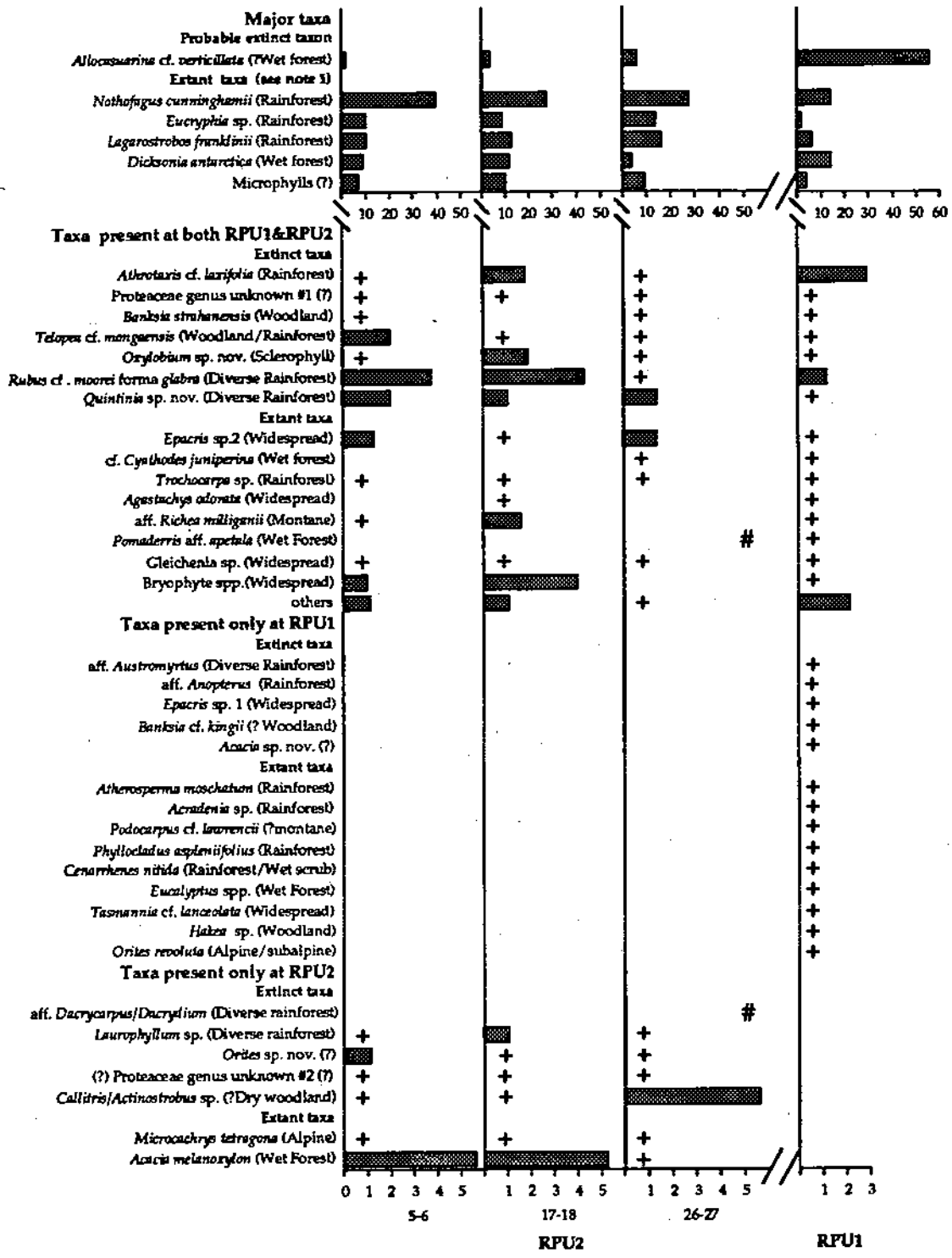


Figure 4.3 : Percentage occurrences of fossil organs in the RPU1 (right hand side) and each of three fossil rich layers in the RPU2 sediments (left hand side). The main modern habitats of the species (or of their close relatives in the case of extinct taxa) are included in brackets after the names. # indicates that the taxon was found outside the counted samples. + indicates <1%. Note that there are two scales.

the densely fossiliferous strata in RPU2. The proportions are based on counts of 3060 macrofossils for RPU1, and 696, 1046 and 720 macrofossils respectively for HF macerated samples of the layers at 5, 17 and 26 cm depth in RPU2. An additional 1601 macrofossils were isolated from the RPU2 sediments, from the less densely fossiliferous strata and from fragments of the leaf rich layers not included in the counts. Only two extra taxa were found among these additional fossils, *Dacrycarpus/Dacrydium* and *Pomaderris ? apetala*. *Pomaderris ? apetala* was found by splitting a rock and was not identified from macerated samples. *Pomaderris* is particularly unlikely to have been identified from macerated samples, since the leaves were fragile, and the cuticle was very poorly preserved. *Dacrycarpus/Dacrydium* was derived from maceration of relatively fossil poor strata of RPU2.

There is no evidence of significant differences between the strata of RPU2. The differences between the proportions of the major taxa are small. There are few significant differences between the proportions of other taxa (*Acacia melanoxylon* and *Rubus* cf *moorei* forma *glabra* are more common, and *Callitris/Actinostrobus* is less common in the 26-27 cm stratum than in the other strata, and a few taxa are absent in one or two strata and present in the others). These differences may be the result of slight taphonomic differences, or chance. RPU2 will therefore be treated as a single unit for the reconstructions.

4.3.2.2 : Regency

Figure 4.4 shows the proportion of macrofossil taxa found in the core at each 10 cm section of the core. No taxa were identified from the dispersed cuticle preparations that were not found as macrofossils, and the proportions were very similar to those for macrofossils, and they are therefore not illustrated.

Eucalyptus fruit of at least two taxa were found in the sediments (*E.* cf. *subcrenulata*, and another taxon which resembled members of *Eucalyptus* section *Obliquae*, e.g. *E. regnans*). The second taxon was most common above 40 cm in the sediments.

The variation in size of *Nothofagus cunninghamii* leaves described in

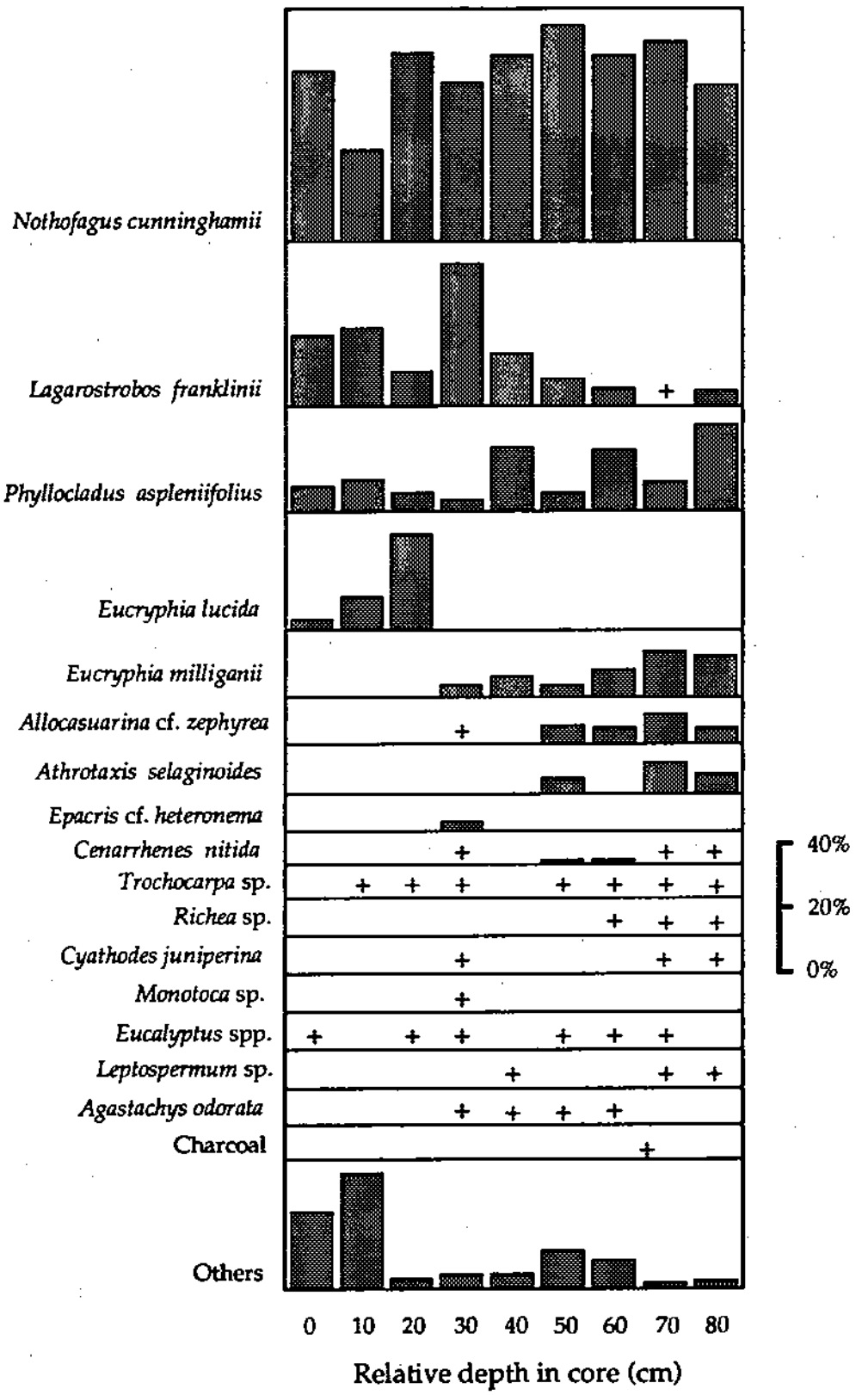


Figure 4.4 : Percentage occurrences of fossil organs in each 10 cm layer of the Regency sediments.

Fitzsimons *et al.* (1990) was not found in this study, and this is discussed in chapter 5. The marked change-over noted in Fitzsimons *et al.* (1990) in *Eucryphia* from small leaved below 30 cm to large leaved forms above 30 cm was confirmed. The small leaved forms were identified as *E. milliganii* and the large leaved forms were identified as *E. lucida* using the cuticle characters described in Hill (1991 b).

4.3.2.3 : Melaleuca Inlet

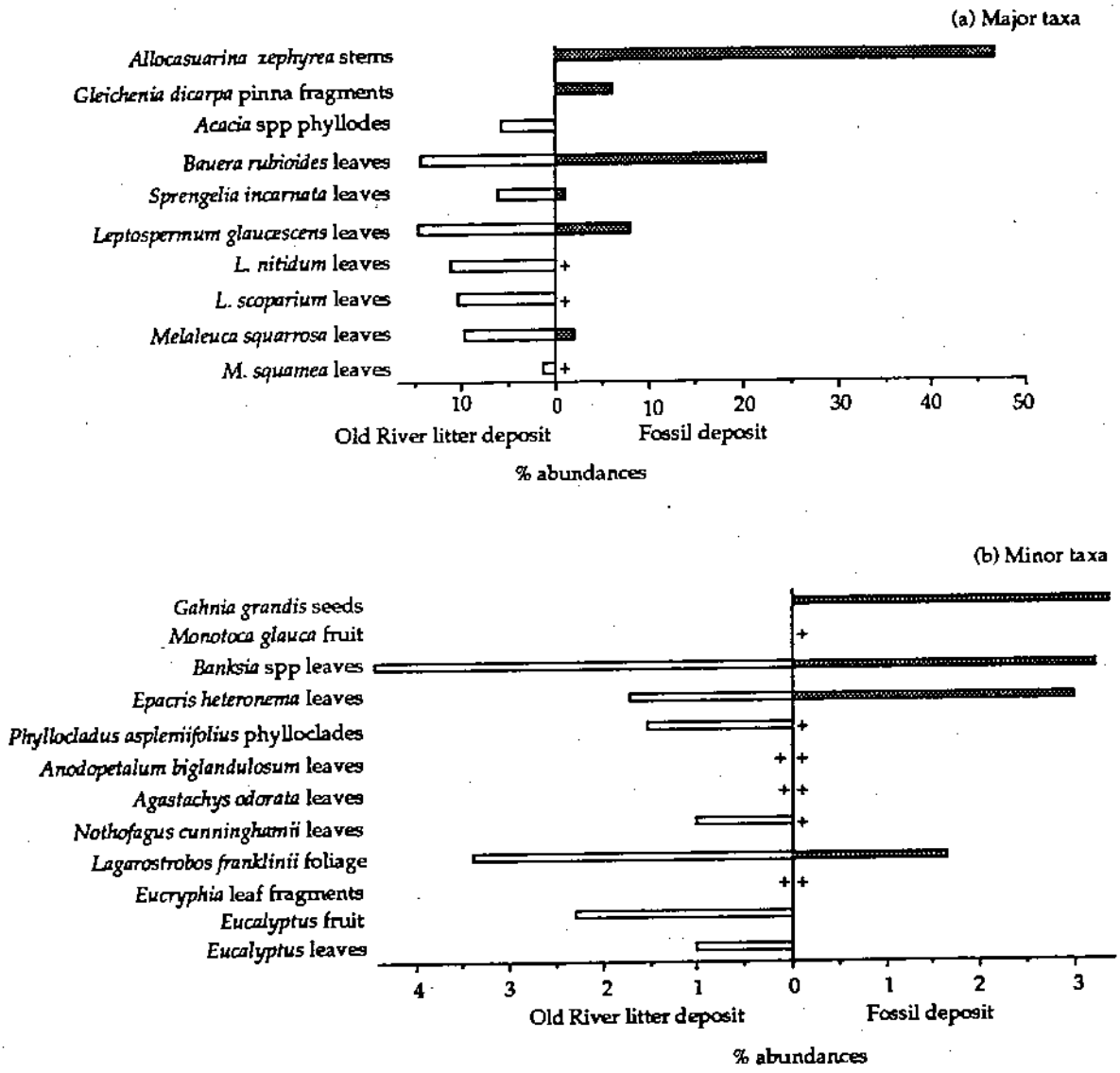


Figure 4.5 : Percentage of identified organs found in water carried litter samples found on the banks of the Old River (left side) and in the Melaleuca Inlet fossil deposit (right side).+ indicates <1%.Note that there are two scales.

Table 4.1 : Fossils extracted from Late Pleistocene sediments at Melaleuca Inlet, south-west Tasmania. Percentages of macrofossil organs are based on a total count of 1342. Percentages of dispersed cuticles are based on a total count of 1357. Percentages of palynomorphs are based on a total count of 577. + indicates less than 1% or the taxon was identified after completion of the count.

Taxon and organ	% abundances macrofossils[1]	dispersed cuticle	pollen[4] &spores
Dicotyledonous Angiosperms			
Asteraceae			
Cassinia aculeata type			+
Caprifoliaceae			
Sambucus gaudichaudiana			+
Casuarinaceae			19
Allocasuarina zephyrea	46.1(1.2)	23	
Cruciferae			+
Cunoniaceae			+[2]
Anodopetalum biglandulosum	+ (+)		1.5
Bauera rubioides	21.1 (1.2)	49	1
Elaeocarpaceae			+
Epacridaceae			
Epacris type		+	
Epacris heteronema	3.0 (+)		1
Epacris spp.	+(+)		
Monotoca glauca	+		6[3]
Sprengelia incarnata	1.0		2[3]
Eucryphiaceae			
Eucryphia sp.		1.5	+[2]
Fabaceae			
Acacia sp.		+	+
Fagaceae			
Nothofagus cunninghamii	+ (+)	+	1
Myrtaceae			
Baeckea sp.	+		
Eucalyptus sp.			1
Leptospermum sp.			5
Leptospermum glaucescens	8.3 (+)	+	
L. nitidum	1.2	+	
L. scoparium	1.3 (+)	1.2	
Melaleuca sp.			5
Melaleuca squamea	+		+
Melaleuca squarrosa	2.0 (+)		
Proteaceae			
Agastachys odorata	+	1.4	1
Banksia kingii	3.2	2.1	3[3]
cf. *Bellendena montana*			+
Cenarrhenes nitida		1.2	+[3]
Hakea sp.		1.5	
Lomatia tasmanica	+	+	
Persoonia			+
Indeterminate Proteaceae			5
Rhamnaceae (not *Pomaderris apetala*)			+
Rutaceae			+
Thymelaceae			
Pimelea			+
Winteraceae			
Tasmannia lanceolata			+

Table 4.1 (cont.)

Taxon and organ	% abundances macrofossils	dispersed cuticle	pollen &spores
Monocotyledonous Angiosperms			
Cyperaceae			21
Gahnia grandis	3.4		
Liliaceae			
Astelia			+
cf. *Blandfordia*			+
cf. *Burchardia*			+
Milligania			+
Restionaceae			2
Gymnosperms			
Podocarpaceae			
Lagarostrobos franklinii	1.6 (+)	8	17
Microcachrys tetragona			+
Microstrobos niphophilus			+
Phyllocladus asplenifolius	+	2.5	12
Ferns and Fern Allies			
Gleicheniaceae			10
Gleichenia dicarpa	+ (1.9)		
Other Ferns and Fern Allies			
Cyathea			+
Dicksonia			+
Histiopteris			+
Lycopodium laterale			+
Microsorum			+
indeterminate	3	5.8	4

Notes : [1] Figures enclosed in brackets are abundances of burnt organs
[2] Pollen of Eucryphiaceae and Cunoniaceae have not been distinguished
[3] Determinations of these taxa are uncertain at the specific level
[4] Pollen identifications and counts made by M.K. Macphail

Table 4.1 lists fossils extracted from the deposit. 1342 macrofossils were recovered. Less than 3% of the total count, belonging to about 6 types, were not identified. In addition, over 1300 dispersed cuticle fragments were extracted (5.8% unidentified) and 577 palynomorphs were counted (4% were not attributed to any family). At this stage it is not known whether the unidentified fossils belong to extant or extinct taxa. Figure 4.5 illustrates the comparison between some of the more important taxa in the Melaleuca Inlet sediments and the Old River litter sample.

4.4 : Discussion

4.4.1 : Vegetation Reconstructions

4.4.1.1 : RPU1

The RPU1 sediments are derived from several blocks of unkown relative stratigraphy. This vegetation, and later, climatic reconstruction, assume that a composite reconstruction gives a reasonable impression of the conditions at the time of deposition of each stratum. This is a reasonable assumption since the composition of common taxa was similar for each block, and was apparently similar within the blocks. The proportions of taxa present in the sediments are consistent with a vegetation composed of forest with a high proportion of rainforest trees, but also sclerophyllous elements, which are similar to the composition of those of modern riparian forest in western Tasmania.

The major rainforest taxa in the sediments are similar to those found in much modern forest in western Tasmania (*Nothofagus cunninghamii*, *Eucryphia* sp., *Lagarostrobos franklinii*, *Athrotaxis* sp. and *Dicksonia antarctica*). Two other major tree species of modern rainforest, *Atherosperma moschatum* and *Phyllocladus asplenifolius*, are present but rare in the sediments. Only *Anodopetalum biglandulosum* is notable by its absence, and the *Athrotaxis* species differs somewhat from any of the three modern species. The rarity of *Atherosperma moschatum* and absence of *Anodopetalum biglandulosum* can be explained in taphonomic terms (see above). The rarity of *Phyllocladus asplenifolius*, however, indicates that this species was probably rare in the source vegetation, or distant from the deposition site, since *P. asplenifolius* is very well represented in many

Pleistocene macrofossil sites, and appears to be well represented in modern sediments (see above). Fossils of several modern rainforest understorey shrub taxa are present in the sediments (*Cenarrhenes nitida*, *Trochocarpa* spp., *Acradenia frankliniae*, *Agastachys odorata* and *Tasmannia lanceolata* all occur as undershrubs in rainforest). The diversity of the rainforest component of the vegetation was greater than modern riparian vegetation (chapter 6). In particular the understorey was probably more complex, with the presence of the probable shrubs aff. *Austromyrtus* and *Quintinia* and the rainforest climber *Rubus*.

Sclerophyll elements are also present in the sediments. Modern *Pomaderris apetala* is typical of wet sclerophyll forest. *Eucalyptus* spp., *Cyathodes juniperina* and *Hakea* spp. are common in modern wet and dry sclerophyll forests. *Pomaderris* species (especially *P. apetala*) and many *Eucalypt* species are middle successional plants and are usually seen in regrowth forest after fire. The presence of *Eucalyptus* sp., *Pomaderris* aff. *apetala* and charcoal in the sediments, indicate that fire was present, and fire adapted species were present in the vegetation. *Allocasuarina* cf. *verticillata* dominates the macrofossil counts, and is likely to have been a dominant tree in wet forest. The presence of strongly sclerophyllous taxa (*Acacia* sp. nov., *Banksia strahanensis*, *B.* cf. *kingii*, *Oxylobium* sp. nov., *Epacris* species) and several unidentified microphyllous taxa is consistent with lowland riparian vegetation.

The macrofossils are therefore likely to have been derived from riparian forest, which was similar to modern western Tasmanian riparian forest, except that the rainforest flora was more diverse (see chapter 6), and some now extinct sclerophyll taxa occurred (see chapter 6).

4.4.1.2 : RPU2

The vegetation appears to have been composed of similar communities as RPU1. Several species, however, are different and a higher proportion of fossils of rainforest taxa is present. The same major taxa occur as in RPU1, except that *Allocasuarina* is much less common, and the rainforest taxa are correspondingly higher. *Eucalyptus* has not been found, but there are strong indications of wet sclerophyll forest.

Pomaderris apetala is now a characteristic species of wet sclerophyll forest and *Acacia melanoxylon* is common in this vegetation type. *Allocasuarina* cf. *verticillata* is likely to have been a wet forest species. Other taxa which are now common in wet forest occur in the sediments, including aff.*Cyathodes juniperina* and *Dicksonia antarctica*. Like RPU1 the rainforest component of the vegetation was more diverse than in modern western Tasmanian riparian forest (chapter 6). Both ground mosses (*Thuidium*, *Ptychomnion aciculare* and possibly ? *Trachyloma*) and pendulous epiphytic mosses were present (*Weymouthia mollis* and *Barbella*) were present. Mosses are a prominent part of Tasmanian wet forest.

The riparian vegetation near Regatta Point at the time of deposition of the RPU2 sediments, therefore, probably contained a higher proportion of rainforest, and less sclerophyll vegetation than at the time of RPU1.

4.4.1.3 : Regency

The macrofossils found in this study are, in general, consistent with the reconstruction presented by Fitzsimons *et al.* (1990). The presence of *Eucalyptus* species in the sediments confirms the local presence of this taxon. The identification of *Eucalyptus* fossil pollen is often tentative, since *Eucalyptus* pollen is under-represented, poorly preserved and resembles the pollen of some other myrtaceous taxa.

There is clearer evidence than presented in Fitzsimons *et al.* (1990) of the local presence of sclerophyll taxa at the time of deposition. In particular, the identification of epacridaceous species is more decisive. Epacridaceous microphylls now occur in a wide range of habitats including rainforest (e.g. *Trochocarpa* spp. and *Archeria* spp.), wet forest and woodland (e.g. *Richea* spp., *Monotoca* spp. and *Cyathodes juniperina*) and sclerophyllous heaths (e.g. *Epacris* spp.). The sediments include each of these type of microphyll.

The casuarinaceous fossils in the sediments are all similar to *Allocasuarina zephyrea* which is now widespread in western Tasmania in heath and sedgeland/heath communities.

4.4.1.4 : Melaleuca Inlet

The array of macrofossil species in the Melaleuca Inlet sediments suggests more than one vegetation type contributed to the assemblage. The lens appears to have been deposited in a river, and therefore may contain plant organs from riparian vegetation some distance upstream, thus explaining an input by more than one vegetation type. The deposit contains elements now generally found in rainforest (*Nothofagus cunninghamii*, *Eucryphia lucida* and *Anodopetalum biglandulosum*), in sclerophyll forest and scrub (*Leptospermum glaucescens*, aff. *Monotoca glauca* and *Gahnia grandis*) and in sedgeland-heath (*Leptospermum nitidum*, *Epacris heteronema* and *Sprengelia incarnata*). Other species frequently occur in more than one of these vegetation types. Within the loose comparisons permitted by taphonomic studies, the proportions of taxa in the fossil deposit are sufficiently similar to those from the Old River litter sample to allow us to use this site for comparison. Both contain large amounts of *Bauera rubioides* and *Leptospermum glaucescens* and have comparable amounts of *Melaleuca* species and *L. scoparium*. These together suggest a dominance of wet scrub, at least along the river banks. The two sites also show comparable amounts of the rainforest species *Nothofagus cunninghamii*, *Phyllocladus aspleniifolius* and *Lagarostrobos franklinii*. The rainforest is distant from the Old River site and I infer that rainforest was either distant from the fossil site or it comprised only a small part of the local vegetation, particularly since these species tend to be over-represented in sedimentary environments.

The macrofossil analysis of the Melaleuca sediments is consistent with the microfossil assemblage described in Jordan *et al.* (1991) which suggests a local and regional vegetation dominated by scrub and sedgeland-heath, with some rainforest.

4.4.2 : Climatic reconstructions

4.4.2.1 : RPU1

There are floristic elements in the Regatta Point leaf bed (RPU2) sediments which are consistent with several different climatic interpretations. The majority of both fossil specimens and fossil taxa are consistent with climatic conditions similar to those which now prevail on the

west coast of Tasmania. There are also elements which could be interpreted as meaning that conditions were warmer than at present (the rainforest taxa aff. *Austromyrtus* and *Rubus* cf. *moorei* forma *glabra*, and the sclerophyll taxa *Banksia strahanensis* and *Oxylobium* sp. nov.). There are, however, some elements which suggest cooler conditions prevailed than at present. *Orites revoluta* is now a high altitude species, but long distance transport cannot be excluded for this taxon since only a single leaf was found of this sclerophyllous small leaved species. *Cyathodes juniperina* and *Tasmannia lanceolata* are more common in high altitude areas than in lowland forest. *Podocarpus* cf. *lawrencii* and aff. *Richea milliganii*/*R. acerosa* are similar to high altitude species.

There is, however, a reasonable explanation for these apparently conflicting lines of evidence. Each of the indicators of cooler climate, and the rainforest species indicators of warmer climate all live in areas with little or no summer drought. *Rubus* cf. *moorei* , *Podocarpus* cf. *lawrencii* and *Quintinia* sp. nov. also have similarities to taxa growing in the nearly everwet forests of western New Zealand. Hence, this flora may represent a flora which was less drought adapted than the current lowland western Tasmanian flora. This may indicate that the climate at the time of deposition was less prone to summer drought than at present. However, it may indicate instead that the summer drought intolerant taxa have been eliminated by dry periods of many glaciations, but could satisfactorily survive under current conditions in western coastal Tasmania.

There is no reason to believe that the climate at Regatta Point at the time of deposition of the RPU1 sediments differed greatly from the modern climate there, except that the climate may have been less seasonally dry, and possibly warmer. The floristic indications of these differences may have been results of differences in climatic history rather than the current conditions at the time of deposition.

4.4.2.2 : RPU2

Very similar climatic arguments to those presented for RPU1 can be applied to RPU2. Most of the species mentioned in these arguments are present in the RPU2 sediments, but a few others are present. *Microcachrys*

tetragona is now restricted to alpine areas, but it thrives in cultivation under warmer conditions than prevail in western Tasmania, provided abundant water and sufficient light are available. Aff. *Dacrycarpus/ Dacrydium* appears to have its closest affinities with New Zealand species. *Laurophyllum* species appears to be a strong indicator of climates warmer than at present since it is likely to have been well dispersed, and the broad leaved Lauraceae no longer occur in southern Australia or southern New Zealand (see Figure 3.38). As argued in chapter 3, the presence of *Callitris/Actinostrobus* may indicate warmer, wet conditions rather than the dry habitats mostly occupied by these genera. Floristics therefore indicates that conditions at the time of deposition of the RPU2 sediments may have been warmer than at present, but probably as wet or wetter in this area.

4.4.2.3 : Regency

The macrofossil floristic composition of these sediments is consistent with the climatic interpretation of Fitzsimons *et al.* (1990) which was that after the 40 cm layer was deposited conditions were wet at all times, but probably as wet as or wetter than at present and as warm as or warmer than at present in this area, and conditions were cooler and drier before the 40 cm layer was deposited than after. The macrofossil evidence discriminating the layers include the change from *Eucryphia milliganii* to *E. lucida*, and the loss of *Athrotaxis selaginoides* indicating warming of the climate at about 30-40 cm. The apparent loss of sclerophyll taxa (*Leptospermum*, *Allocasuarina* sp., aff. *Cyathodes juniperina* and *Agastachys odorata*) around this time may indicate a trend towards wetter conditions, warmer conditions, lower fire frequency, or any combination of the three. The higher proportion of charcoal in the sediments below 30-40 cm (Fitzsimons *et al.* 1990) indicates that fire frequency probably did decline after the 30-40 cm layers were deposited. The relatively high proportions of pollen of the now strictly alpine/sub-alpine conifer *Microstrobos niphophilus* and other upland taxa before the 40 cm stratum was deposited (Fitzsimons *et al.* 1990) together with macrofossil floristic evidence strongly supports changes in vegetation consistent with increased temperatures and precipitation around the time of deposition of

the 40 cm stratum of the Regency sediments.

4.4.2.4 : Melaleuca Inlet

The effects of glacial history are less likely to distort the floristics-based climate reconstruction at Melaleuca Inlet, than at Regatta Point, since the time of deposition of the Melaleuca Inlet sediments was after most of the Pleistocene glaciations, and species are unlikely to change their ecological preferences greatly in the relatively short time between then and now. There are several features that suggest that the climate at Melaleuca Inlet at the time of deposition is likely to have been as cool as or cooler than it is now :

1. The present day distributions of all extant species listed, except *Sambucus gaudichaudiana*, are consistent with such a climate and there are several features which suggest a cooler climate than at present.

2. The extinct species *Banksia kingii* shows affinities with *B. saxicola* A. S. George and *B. canei* J. H. Willis of Victoria and New South Wales(Jordan and Hill 1991). It has a very thick lamina, cuticle and petiole. These traits are positively correlated with altitude in *Banksia* series *Salicinae* but are more extreme in the specimens from Melaleuca than in any specimens of this series examined (G. J. Jordan, unpublished data). In these traits the fossil most closely resembles high altitude forms of these species, e.g. *B. saxicola* from Mt. Williams (about 1200 m) in the Grampians in Victoria, and *B. canei* from the Kybean Range (about 1250 m) in N.S.W. Leaves of *Banksia marginata* from Mt. Williams and similar habitats have much thicker cuticle, lamina and petiole than leaves of populations in lowland south-west Tasmania, and hence these changes in morphology are likely to have resulted from the effects of decreased temperature. Increased wind abrasion, higher insolation or periodic desiccation are less likely to be the causes of these morphological traits since the Melaleuca Inlet site was lowland and apparently at least as wet as it is now.

3. The leaf size and cuticle morphology of *Anodopetalum biglandulosum* from the deposit is outside the range of present day low altitude forms of the species, and is consistent with some high altitude forms (e.g. from Mt. Read, 1140 m). The leaves of other taxa also tend to be

smaller than those of the present day members of these taxa currently in the same area. This, however, may be a preservational artefact, since small leaves are probably more likely to survive the processes of preservation.

4. The presence of currently alpine taxa such as *Microstrobos niphophilus* and a species of *Astelia* may be significant, although these taxa only occur as pollen and may therefore have reached the sediments through long-distance dispersal.

The present distributions of the identified taxa are consistent with a climate as wet as or wetter than the current one at Melaleuca Inlet. In particular, many of the species, including *Agastachys odorata*, *Epacris heteronema*, *Eucryphia* species and *Lagarostrobos franklinii* are now restricted to the wetter parts of Tasmania.

There is independent geological evidence which strongly suggests the presence of high levels of precipitation. The lens was found between facies of river gravels and stones, indicative of much fluvial activity. As the regional topography in the Pleistocene would have been almost identical to now it is assumed that the deposition of such sediments in a possible braided river situation was a consequence of high rainfall.

Site	Inferred climate	Inferred vegetation
Melaleuca Inlet	Mean temperature ≤ now Mean rainfall ≥ now	Mosaic vegetation including small amounts of cool temperate rainforest, but primarily scrub/heath. *Banksia kingii* present, *Allocasuarina* more prominent than today.
Regency	Mean temperature ≥ now Mean rainfall ≥ now	Cool temperate rainforest/wet sclerophyll vegetation. Some extinct rainforest components (*Quintinia*, Loranthaceae). *Allocasuarina* more prominent than today.
Regatta Point 1	Mean temperature ±= now Mean rainfall ≥ now	Mosaic riparian vegetation, rainforest and sclerophyll elements prominent. Extinct sclerophyll and rainforest taxa present.
Regatta Point 2	Mean temperature (?) ≥ now Mean rainfall ≥ now	Mosaic riparian vegetation, rainforest prominent, sclerophyll present. Extinct sclerophyll and rainforest taxa present.

Table 4.2. Summary of inferred vegetation and climate for each fossil site.

Chapter 5 : Climate and Leaf Size of *Nothofagus cunninghamii*

5.1 : Introduction

The association of temperature and precipitation with leaf size has been known for a long time (e.g. Bailey and Sinnott 1916). The inverse relationship of leaf length with latitude and/or altitude is well known. This gradient, of course, is also a gradient of increasing temperature and since growth rates increase with increasing temperature, it has been assumed that temperature difference is one of the main causes of differences in leaf size. Increasing mean leaf size with increasing local temperatures have been shown between species within genera (e.g. Hill and Reid 1987) and between whole floras (e.g. Christophel and Greenwood 1987). The relationship between populations within species with temperature is less well known. This trend is overlain by a trend towards larger leaf size with increased precipitation. This response in leaf size with increasing precipitation is a saturating curve (i.e. there tends to be little change in leaf size with changes in precipitation for high precipitation) (Givnish 1987). Webb (1959) used leaf size to define the primary split in his classification of rainforest types. If rainfall is sufficient this primary split appears to be determined by temperature, through either altitude or latitude (Webb 1968). Webb's physiognomic classification has been adopted widely by other workers in both palaeoecology and neoecology.

There have been several attempts to correlate leaf sizes of whole floras with temperature in order to predict past climates (e.g. Davis and Taylor 1980; Evans 1991). Christophel and Greenwood (1989) related leaf size of forest floor litter to temperature related forest structures. The use of leaf litter has the advantages over the use of on-plant leaves of allowing objective sampling, of producing samples integrated over the whole local vegetation, and producing samples more closely related to fossil in sediments. Studies of northern hemisphere physiognomy indicate that leaf margin type is the best predictor of palaeotemperature (Wolfe 1971, 1979) but Christophel and Greenwood propose that leaf length is a better indicator of palaeoclimate in Australia. None of these have made any serious attempt to attach confidence intervals to these estimates. Dolph and

Dilcher (1980) proposed that the relationship between leaf size and temperature had little or no predictive power for fossil or present climates, but their studies were limited in number of sites and to tropical areas. Broader studies would increase the chance of finding relationships.

A concern in the use of physiognomy (and floristics and other biologically based methods) to predict palaeoclimates, is the possible effect of ecological lag (i.e. that living systems are not in equilibrium with their environments, rather they are always catching up). Cole (1985) demonstrated an apparent lag in the response of vegetation diversity to the climate changes late in the Last Glacial and in the Holocene. Markgraf (1986) argued that these diversity changes were probably a result of other effects, and did not necessarily represent ecological lag, but these criticisms appear to be largely unfounded (e.g. Cole 1986). There is considerable further evidence of ecological lag in floristics (Davis 1986). The lags in response times are likely to be different for different species (e.g. Davis 1987). The main temperate and Boreal forest tree species of North America appear to show a lag time in colonization of a few hundred years behind the climate changes (e.g. Schoonmaker and Foster 1991). However, the impact of Quaternary glaciations on these forests is likely to have been very severe, with widespread deforestation. Tasmania, however, almost certainly had a more maritime climate than continental Northern Hemisphere, a virtually impassable barrier to dispersal (Bass Strait), and great local differentiation of habitat. Strategies of coping with environmental change other than rapid dispersal may have been favoured under these conditions. Lags in physiognomy are less well understood, but three factors are likely to contribute, phenotypic plasticity, the variability of the local gene pool, and time for invasion of new genes. The first response lag will be within a year or two. The second will be within generations, depending on the strength of selection. The size of the lag derived from the third will depend on dispersal ability of pollen and seed, and the advantage local populations have over invading genotypes (in numerical superiority of seed and pollen).

Attempts to relate climate to the physiognomy of leaf litter of whole floras of cool temperate forests of south-eastern Australia are questionable because these floras are very species poor. In particular, rainforest leaf litter

from much of Tasmania and southern Victoria tends to be dominated by one species (*Nothofagus cunninghamii*). Since each taxon is likely to respond to climatic conditions differently, samples dominated by one, or a few species are likely to be strongly biased. The Regatta Point and Regency sediments have numerous, well preserved *N. cunninghamii* leaves. These leaves also have the advantage of being easily and reliably identified. The leaves of *N. cunninghamii* in the Regatta Point sediments also seemed to be more variable than modern populations. This study therefore investigates the relationship between climate and the physiognomy of *N. cunninghamii* leaves, firstly to attempt to predict palaeoclimates, and secondly to detect signs of ecological lag. Other Pleistocene and Holocene sediments also contain numerous well preserved *N. cunninghamii* leaves, so there are avenues for future progress in this work.

5.2 : Materials and Methods

5.2.1 : Leaf morphometrics

Litter samples were collected from the floors of forests containing *Nothofagus* subgenus *Lophozonia* from throughout its extant range in Australia, that is *N. cunninghamii* in Tasmania and Victoria (see Fig. 5.1), and *N. moorei* in New South Wales and Queensland. A litter sample containing the only New Zealand species of the sub-genus *N. menziesii* was collected from Paparoa. These three species are the only evergreen species in sub-genus *Lophozonia*. Sites within Australia were chosen to cover the present climatic range of these species. There were six litter samples containing *N. moorei*, 15 samples containing *N. cunninghamii* from Victoria and 39 samples containing *N. cunninghamii* from Tasmania. Each sample was a composite of the litter from at least five 0.1 m^2 plots randomly placed in a 1000 m^2 area of forest floor. Each sample was subdivided evenly* until a small subsample containing at least 30 leaves was produced. The lengths and widths of all measurable *Nothofagus* leaves in this subsample were measured. In some samples subsamples of at least 120 leaves were measured to study the distributions of the leaf measurements.

* by spreading the sample evenly on a tray in one direction and splitting the sample in half along this same direction, and repeating this procedure

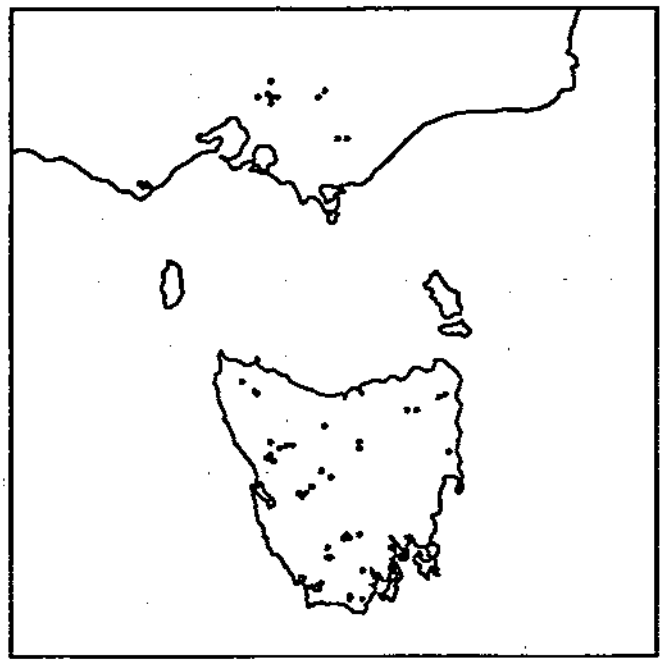


Figure 5.1 : Location of *Nothofagus cunninghamii* litter samples.

Leaf lengths and widths of all measurable leaves recovered from the RPU1 sediments, and from each of the leaf beds from RPU2 were measured. Length was measured on 289 leaves, and width on 315 leaves from RPU1. Length and width was measured on more than 100 leaves from each of the RPU2 samples. From the Regency sediments at least 50 leaves were measured from each 10 cm length of core, except at 0 and 40 cm where preservation was poor and only 10 and 33 leaves were measurable. In three very well preserved strata (20, 60 and 80 cm) at least 150 leaves were measured for distributional analysis.

The sample variances of the leaf lengths and widths of the extant sites were correlated with the sample means. The measurements, therefore, were log transformed. The residuals of one way analyses of variance of the transformed measurements between samples were then approximately normal and sample variances were independent of the means.

The distributions of the log transformed leaf lengths of several litter sites, RPU1, each stratum of RPU2, and three strata from Regency were studied using the program MIX, which fits mixtures of distributions to

histogram data (MacDonald and Green 1988). The program chooses combinations of prescribed numbers of normal (or other) distributions using maximum likelihood methods for categorical data. The leaf length data was therefore grouped into categories of 0.05 log10(mm). Optimal combinations of three, two and one normal distributions were fitted in this way to the leaf lengths for each of these sites. In some cases optimal combinations of three distributions, and occasionally of two distributions, were not calculable, but only where any component distributions were highly overlapping, and of no interest in this work. The means, standard deviations and proportions of the total of each of the component distributions were not constrained. Goodness of fit chi-square statistics were calculated for each fitted mixture of distributions. Fitting two normal distributions to the data, as opposed to one removed a constraint which decreases the chi-square and the degrees of freedom. The significance of the constraint was then tested as a chi-square equal to the difference in chi-square with degrees of freedom equal to the change in degrees of freedom produced by removing the constraint (MacDonald and Green 1988). Distributions were assumed to be unimodal unless the reduction in chi-squared associated with fitting two or three normal distributions instead of one was significant. The remaining distributions were then assumed to be bimodal unless fitting three normal distributions instead of two produced a significant reduction in chi-square.

5.2.2 : Climate estimates from *Nothofagus* leaf morphology

Climatic parameters were estimated using BIOCLIM (e.g. Busby 1988) for each of the *N. cunninghamii* and *N. moorei* sites. Mean monthly precipitation, minimum and maximum temperature are estimated by this program which fits climatic surfaces between meteorological stations. Sixteen climatic parameters of possible ecological importance are then derived from these estimates. The relevant parameters were estimated for the New Zealand *N. menziesii* site by interpolation between climatic averages (New Zealand Meteorological Service 1987) for two stations near the west coast (Greymouth to the south, and Westport Airport to the north of the site). This interpolation is likely to give reasonable estimates for temperature parameters.

Regressions of log transformed leaf length on mean temperature of the warmest quarter were calculated using the regression with replicates method described in Sokal and Rohlf (1981), using SAS (SAS Institute Inc. 1988 c). Temperature estimates with confidence intervals were calculated using the inverse prediction method (i.e. predicting x from y rather than the more usual y from x) of Sokal and Rohlf (1981). Of the multitude of regressions between climatic parameters and leaf measurements that could be fitted, log of leaf length on temperature of the warmest quarter alone was used for the following reasons :

(1) choosing the best regression from many combinations invalidates the estimates and confidence interval calculated by this method. It is therefore necessary to choose the variables to be regressed *a priori*,

(2) leaf lengths alone was used rather than leaf widths because leaf lengths showed greater relative variation between samples than leaf widths for fossil and extant *Nothofagus* leaves,

(3) a linear combination of the two measurements derived from discriminant analysis was not used because both leaf length and width could be measured on many fewer fossil leaves than just leaf length. The fossil leaves for which both leaf length and width could be measured also showed a strong bias towards small leaves, and

(4) temperature of the warmest quarter is the BIOCLIM parameter most strongly correlated to log transformed leaf lengths of litter of whole floras from a wider range of wet climates (Tilyard 1992). *Nothofagus cunninghamii* now only occurs in wet climates (regions with average precipitation greater than 1000 mm per annum at least 50 mm in the driest month (Busby 1984)). Log transformed leaf length is poorly correlated with winter temperature. There is also evidence of curvature in the regressions of log transformed leaf lengths in litter of whole floras on other BIOCLIM parameters, whereas there is no evidence of curvature in the regression of log transformed leaf length on temperature of the warmest quarter. All the sites are from moderate to high precipitation areas, so temperature is likely to have a stronger influence than precipitation on leaf size (e.g. Givnish 1987). In the habitat of *Nothofagus* subgenus *Lophozonia* in Australia (cool temperate rainforests and montane habitats), temperature of the warmest quarter is

likely to be the period of optimum production, because winter temperatures are too low, even though water availability is greater in many of these areas in winter. Southern cool temperate forests have winter dominated rainfall, but *N. cunninghamii* is restricted to areas with predictable, and moderately high summer rainfall (e.g. Busby 1984), and at the low summer precipitation range it is restricted to gullies with wet aspect. It is likely therefore, that the production of *Nothofagus* subgenus *Lophozonia* is restricted by temperature in summer rather than water availability. Hence, there is independent evidence that leaf length is best related to temperature of the warmest quarter (from the whole flora litter sample measurements) and reasons to believe that this season is the period of optimum production. Among the parameters available to this study, temperature of the warmest quarter is, therefore likely to be the strongest climatic determinant of leaf-size in *N. cunninghamii*.

5.2.3 : Taphonomic Analysis

The analysis presented here estimates the relationship between the lengths of *N. cunninghamii* leaves in forest floor litter and a climate parameter. However, the lengths of leaves in fossil sediments may not be the same as the lengths of the leaves in litter on the floor of the source vegetation. This work assumes that the bias in climatic estimates made by comparing fossil leaves with extant forest floor litter falls within predictable bounds, and this taphonomic analysis attempts to estimate these bounds by comparing samples from modern sediments with litter samples from the forest floor of the source vegetation. Lengths of *N. cunninghamii* leaves in sediment samples from two lakes (Hastings Pool and Lake Dobson - see chapter 2) and from a litter sample carried by a river for some distance and deposited (Old River) were compared with lengths from litter samples from the forest floors of the source vegetations of the *N. cunninghamii* leaves in the lake sediment and river samples. At least 30 *N. cunninghamii* leaves were measured from each sample. More than 120 leaves from 2 of the Hastings Pool samples and 3 of the Lake Dobson samples were measured for distributional analysis.

The number of *N. cunninghamii* leaves in different samples in the

Lake Dobson sediments varied greatly, from none to several hundred. Only 24 samples out of 156 contained enough measurable leaves so the choice of leaves measured is biased towards those from sites with heavy sedimentation of *N. cunninghamii* leaves. This bias is justified since fossil sites which contain sufficient *Nothofagus* leaves to measure for this analysis are undoubtedly sites where heavy sedimentation of *Nothofagus* leaves has occurred. Samples were also taken from the forest floor from two nearby sites in the catchment of the lake.

Leaves were measured from the litter sample collected from the bank of the Old River described in Chapter 2, and from a litter sample collected from the forest floor of the small patch of rainforest about 2 km upstream of the river bank sample. This rainforest patch is the source of the *N. cunninghamii* leaves in the river bank sample.

Log transformed leaf lengths of sediments were compared with log transformed leaf lengths of the source vegetation litter for each of the sites by analysis of variance using SAS (SAS Institute Inc. 1988 c). A two stratum design with samples nested within the source type (forest or sediment) was used for Lake Dobson and Hastings Pool data where there were replicate samples. There were no replicate samples from the Old River site so a single stratum analysis of variance was used. Distributions of the log transformed leaf lengths were studied using the methods described above for litter and fossil samples. Standard deviations of the sediment and forest floor log transformed leaf lengths were compared in the Lake Dobson and Hastings Pool sediments using a two way factorial analysis of variance.

5.3 : Results

5.3.1 : Analysis of distributions of leaf lengths

Figure 5.2 shows the relationship of the means of log of leaf length to their standard deviations for extant *N. cunninghamii*, *N. menziesii* and *N. moorei* and for *Nothofagus* leaves from the Regatta Point and Regency sediments. There are no trends apparent in this relationship for extant *N. cunninghamii*, and the standard deviations of log leaf lengths of *N. menziesii* and *N. moorei* are similar to those of *N. cunninghamii*. All the standard deviations of extant samples fall within the range 0.7 to 0.15. This

range is therefore inferred to be the normal range of mean log leaf length in litter for extant evergreen *Nothofagus* subgenus *Lophozonia*.

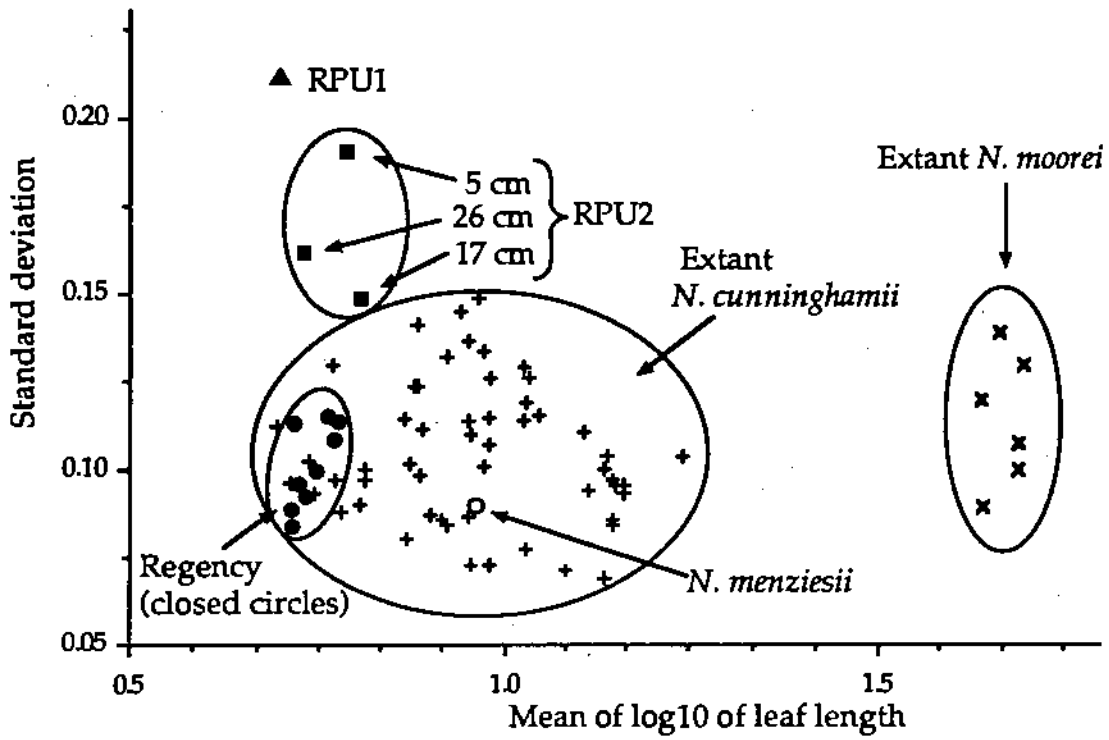


Figure 5.2 : Plot of standard deviations versus means of log transformed leaf lengths of fossil samples of *Nothofagus cunninghamii* and extant forest floor litter samples of *N. cunninghamii*, *N. moorei* and *N. menziesii*. The single *N. menziesii* sample (open circle) and the fossil samples from Regency (closed circles) all fall within the range of the extant *N. cunninghamii* samples (+) in both log of leaf length and standard deviation. *Nothofagus moorei* (X) has larger leaves but similar standard deviations to *N. cunninghamii*. The Regatta Point samples (squares and triangles) show considerably higher standard deviations than any of the extant samples.

Representative distributions of log leaf lengths for fossil and extant samples are illustrated in Figures 5.3, 5.4, 5.5 and 5.6 and the result of the distribution analyses are under each histogram.

Many of the extant forest floor samples do not differ significantly from normal distributions (Figures 5.3 a, b, c & d), but some are consistent with two component normal distributions (e.g. Figure 5.3 e) and one, L. Macintosh (Figure 5.3 f) is consistent with being composed of three normal distributions. Where the component distributions produce relatively distinct peaks (e.g. Figures 5.3 e & f), some variation in sources is assumed. In

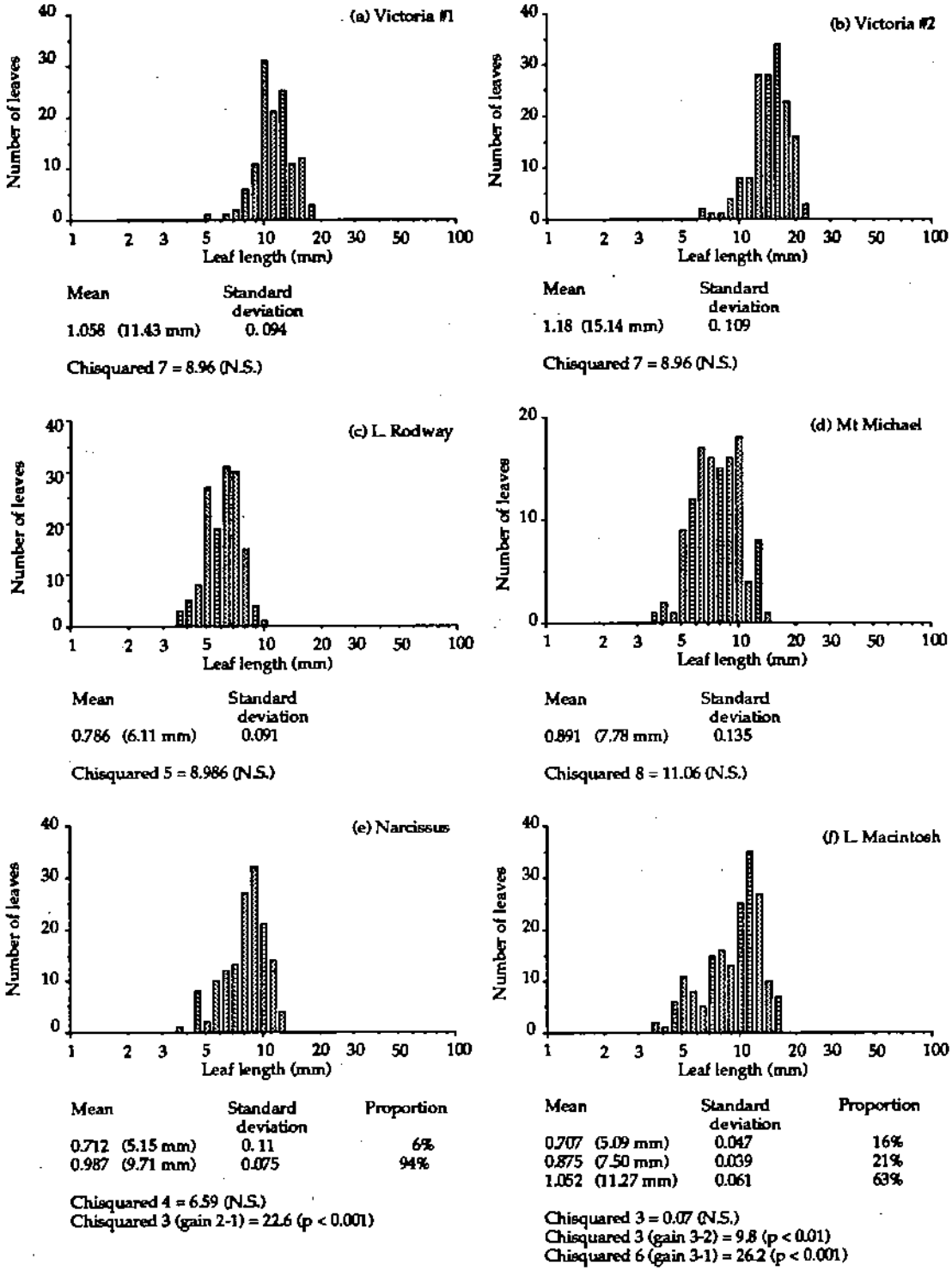


Figure 5.3 : Histograms of leaf lengths (on logarithmic scales) of *Nothofagus cunninghamii* from six extant forest floor litter samples. For each sample the results of the distributional analysis are included at the bottom of the histogram. The means, standard deviations and proportions defining each component distribution are recorded. The number of component distributions is the maximum number for which a significant reduction in chi-square can be attained. The first chi-squared value is the goodness of fit of the mixture of normal distributions defined for each histogram. Gain chi squared values (the reductions in goodness of fit chi-squared attained by fitting two (or three) rather than one distribution) are shown when they are significant.

each sample where distinct significant peaks are present the component distributions have standard deviations lower than the normal range for litter samples as defined above, and the combined standard deviation is not generally in the highest part of the normal range. The presence of multiple peaks may, therefore, to be the result of two or three trees of distinct morphology dominating the sample, and hence merely a sampling artefact. In some cases the distributions are significantly non-normal but there is no evidence of bimodality. This is not taken to be evidence of any mixture in sources.

The distributions of leaf lengths of the sediment samples from Lake Dobson and Hastings Pool are not distinctly bimodal (e.g. Figure 5.4). The distributions from The standard deviations of log transformed lengths for the sediments were not statistically significant from those of the source vegetation leaf litter for each site (Table 5.1). There is, therefore, no evidence that the processes of sedimentation are likely to produce bimodal distributions of log transformed *N. cunninghamii* leaf lengths, or to produce significantly higher standard deviations of log transformed leaf length in sediments than in forest floor litter.

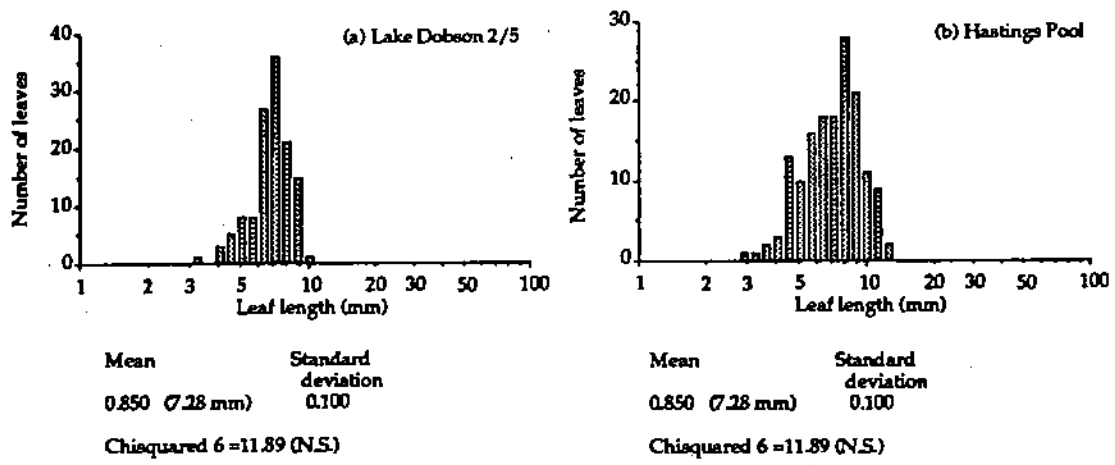


Figure 5.4 : Histograms of leaf lengths of *Nothofagus cunninghamii* from representative samples from the Hastings Pool and Lake Dobson lake sediments. The statistics are explained in the caption for Figure 5.3.

Site	Means of log of leaf length		Difference (forest-sediment)	probability (forest= sediment)	Difference in estimated temperature
	forest	sediment			
Lake Dobson	0.916 (8.25mm)	0.787 (6.12mm)	0.129	< 0.0001	2.63 °C
Hastings Pool	0.88 (7.59mm)	0.841 (6.93mm)	0.039	< 0.01	0.79 °C
Old River	0.958 (9.08mm)	0.9111 (8.15mm)	0.0469	< 0.01	0.96 °C

Table 5.1 : Comparison of means of log transformed leaf *N. cunninghamii* lengths of water borne samples with those of forest floor leaf litter from the source vegetation for three sites. The probabilities are the results of analysis of variances for each site. Differences in estimated temperatures of the warmest quarter are calculated from the regression analysis (see text).

The fossil samples from Regency are consistent with extant *N. cunninghamii*, although they fall into the lower end of leaf length (Figure 5.2). There is no evidence of bimodality of log transformed leaf length for any of the Regency samples (Figure 5.5).

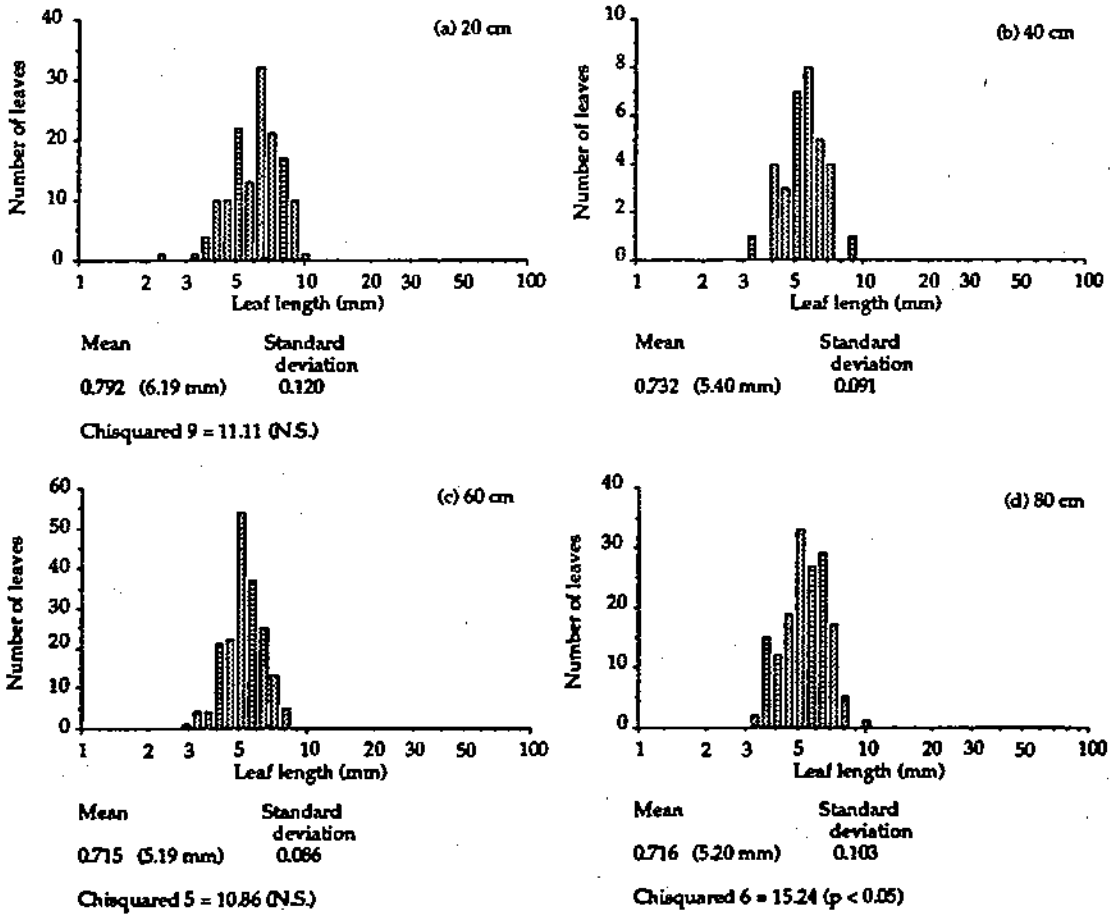


Figure 5.5 : Histograms of leaf lengths of fossil *Nothofagus* for four of the nine Regency fossil samples. The statistics are explained in the caption for Figure 5.3.

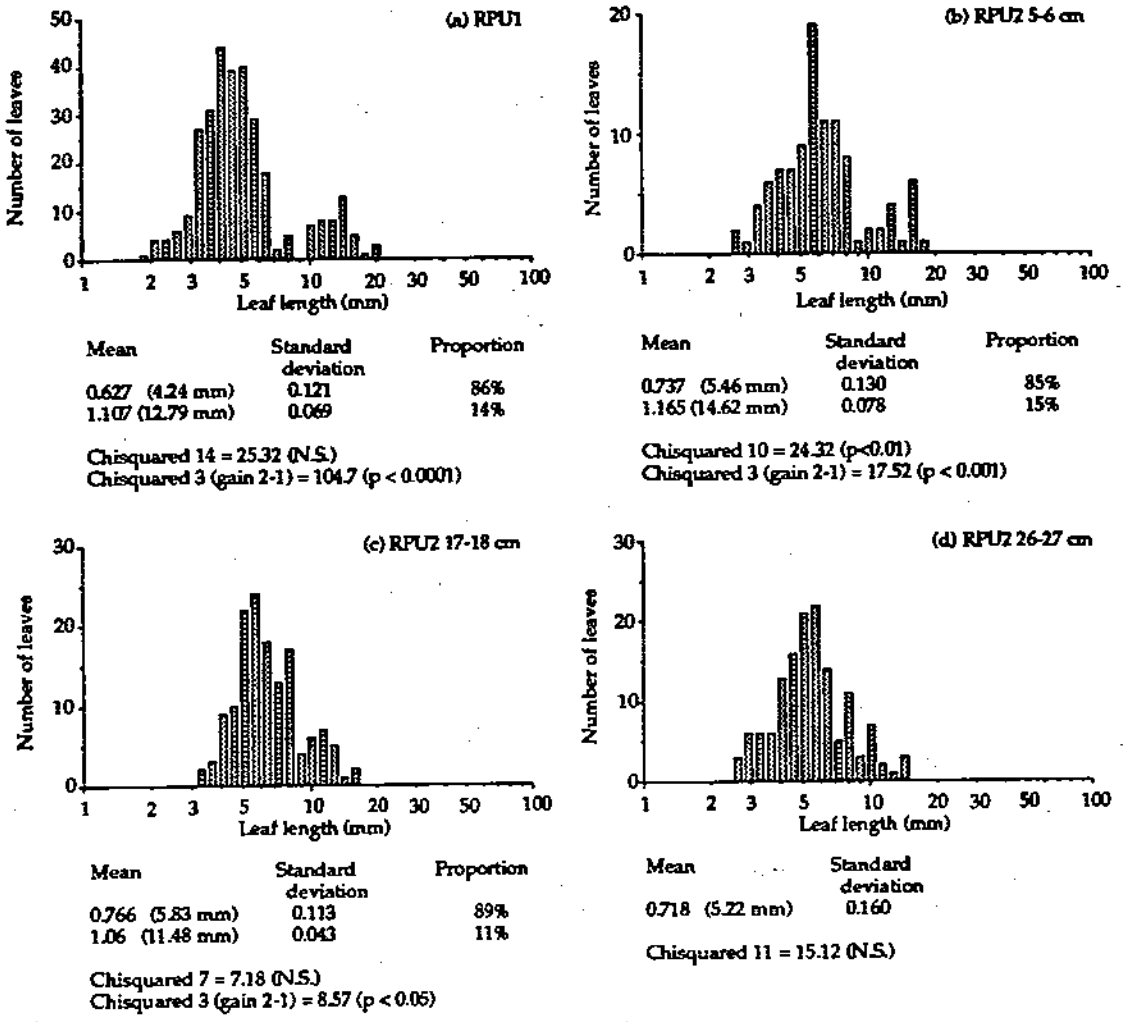


Figure 5.6 : Histograms of leaf lengths of fossil *Nothofagus* from the Regatta Point samples. The statistics are explained in the caption for Figure 5.3.

The *Nothofagus* leaves from the Regatta Point sediments, however, are markedly different to any of the extant samples. Their mean log lengths are at the low end of the range of extant *N. cunninghamii*, but their standard deviations are all notably high (Figure 5.2). The RPU1 sample has a much higher standard deviation than any extant sample, more than twice the mean of extant samples, and about 1.5 times as large as any single extant sample. The distribution of the RPU1 sample is strongly bimodal, with scarcely any overlap of the peaks (Figure 5.6 a). The standard deviations of the two component distributions for RPU1 fall well within the range of extant samples. The standard deviations of the RPU2 samples are high. The

standard deviation of the 5-6 cm stratum is very high, those of the 26-27 cm and 17-18 cm strata are lower, but 26-27 is still higher than any of the extant samples, and 17-18 cm stratum is at the top end of the extant range. The 5-6 cm stratum shows a highly significantly bimodal distribution (Figure 5.6 b), the standard deviations and the proportions of the two component distributions are similar to RPU1, although the difference between the two means in the RPU2 sample is less and hence there is more overlap of the distributions. The 17-18 cm sample has a significantly bimodal distribution, but the differences in the means is smaller again (Figure 5.6 c). The estimated standard deviation of the second peak is below (0.043) the normal range of standard deviations of extant samples, but there is considerable uncertainty in this estimate. The 26-27 cm sample shows no significant evidence of bimodality (Figure 5.6 d).

5.3.2 : Climatic Regression

Figure 5.7 shows the relationship between mean temperature of the warmest quarter and the means of the log transformed leaf lengths of extant litter samples. The corresponding regression equation is :

$$\text{Loglength} = 0.2961 + 0.04915(\text{TWQ}) \qquad R^2 = 0.69$$

Where 'Loglength' is the mean of $\log_{10}$ of leaf length (in mm) and 'TWQ' is the BIOCLIM estimate of mean temperature of the warmest quarter (in °C). The predictive equation can then be deduced :

$$\text{TWQ} = 20.496(\text{Loglength}) - 6.024$$

5.3.3 : Taphonomic analysis

The log transformed lengths of *N. cunninghamii* leaves from sediments from all three sites (Hastings Pool, Lake Dobson and Old River) were significantly ~~longer~~ shorter than those from forest floor of the source vegetations (Table 5.1). Taphonomic biases favouring shorter leaves are common (see Greenwood 1992) in water transported sediments. The differences ranged from 0.04 log(mm) to 0.13 log(mm). These correspond to underestimates of temperature of the warmest quarter of between 0.8 °C and 2.6 °C derived from the equations in the previous section. Temperature estimates from measurements of fossils are likely to give underestimates of between about

0.5 °C and 3 °C (assuming that the differentials between fossils and litter in the source vegetation are similar to the differentials found in this taphonomic analysis). Under extreme taphonomic conditions larger or smaller biases may result.

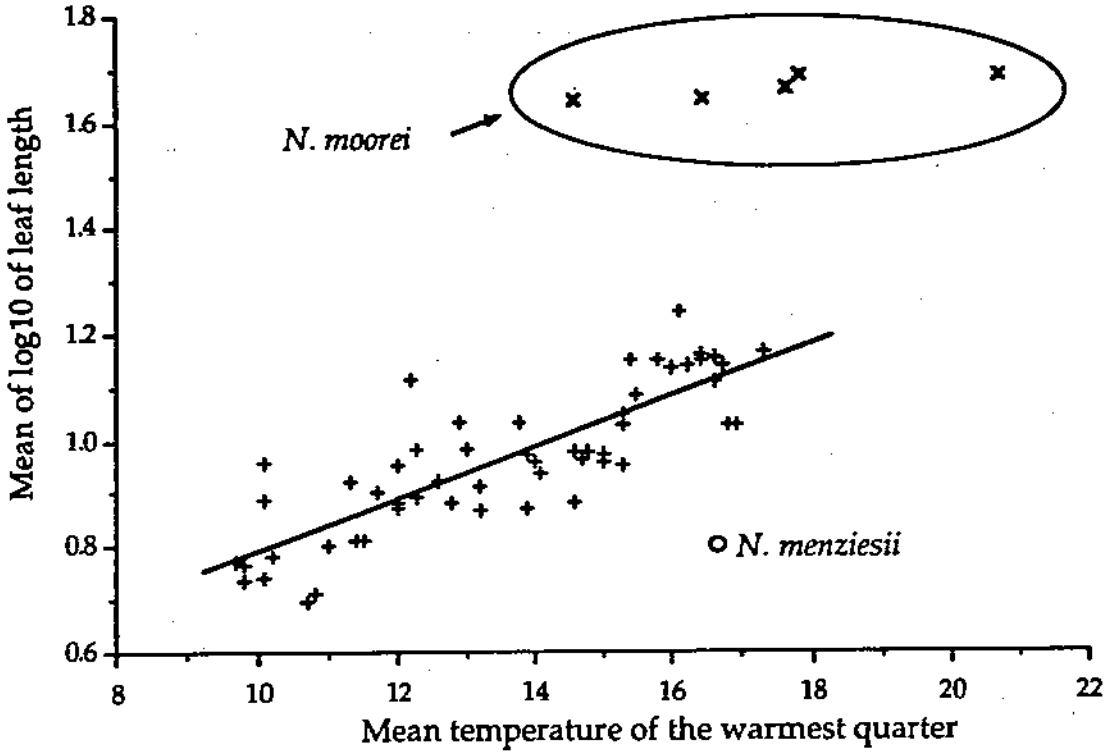


Figure 5.7 : Plot of means of log transformed leaf lengths versus BIOCLIM estimates of the mean temperature of the warmest quarter for *Nothofagus cunninghamii* leaves from extant forest floor leaf litter samples (+). Five comparable samples of *N. moorei* (X) and one of *N. menziesii* (open circle) are also included. The line is the regression line through the *N. cunninghamii* samples.

5.3.4 : Climatic estimates

Table 5.2 gives unadjusted estimates of the mean temperature of the warmest quarter and 95% confidence intervals for each fossil sample. The confidence intervals are very broad (greater than 3 °C for all samples). This is largely due to the relatively poor correlation of mean log transformed leaf length of sites with mean temperature of the warmest quarter (Figure 5.7) even though this is almost certainly close to the best correlated relationship between leaf size and temperature for *N. cunninghamii.*

SITE	Mean log of length (Log10 mm)	Estimated mean temperature of the warmest quarter (°C)
RPU1	0.68	7.8 ± 3.1
RPU2 5-6 cm	0.78	9.8 ± 3.5
" 17-18 cm	0.79	10.1 ± 3.4
" 26-27 cm	0.73	8.8 ± 3.4
Regency 80 cm	0.72	8.7 ± 3.3
" 70 cm	0.72	8.7 ± 4.0
" 60 cm	0.72	8.5 ± 3.2
" 50 cm	0.71	8.5 ± 3.8
" 40 cm	0.73	8.9 ± 4.7
" 30 cm	0.77	9.7 ± 4.2
" 20 cm	0.78	9.8 ± 3.4
" 10 cm	0.75	9.2 ± 4.0
" 0 cm	0.76	9.5 ± 7.2

Table 5.2 : Estimates of the mean temperature of the warmest quarter for the sources of the fossils in the Regatta Point and Regency sediments. The error values are the 95 % confidence intervals. The confidence intervals derived from the regression analysis are not exactly symmetrical around the estimate (Sokal and Rohlf 1981), but in all the cases here are symmetrical within the rounding errors. Note that the confidence intervals are all greater than ± 3° C.

Figures 5.8 a & b give estimates and confidence intervals of the mean temperature of the warmest quarter for each fossil sample adjusted to take into account taphonomic biases. The estimates and 95% confidence intervals derived from the regression analysis have been adjusted to include the estimated effects of taphonomy by increasing each estimate by 1.75 °C (the mean of 0.5°C and 3 °C) and by increasing the confidence intervals by 1.25 °C (the difference between 1.75 °C and either 0.5°C or 3 °C). The confidence intervals, therefore, now include the range covered by increasing the estimate by 0.5 °C and maintaining the confidence intervals, and the range covered by increasing the estimate by 3 °C and maintaining the confidence intervals. This gives very broad confidence intervals, but the main components are derived from the variation around the regression and so the confidence intervals are unlikely to significantly overestimate the uncertainty in the estimates. At both Regency and Regatta Point all the samples give estimates which are lower than modern mean temperatures of

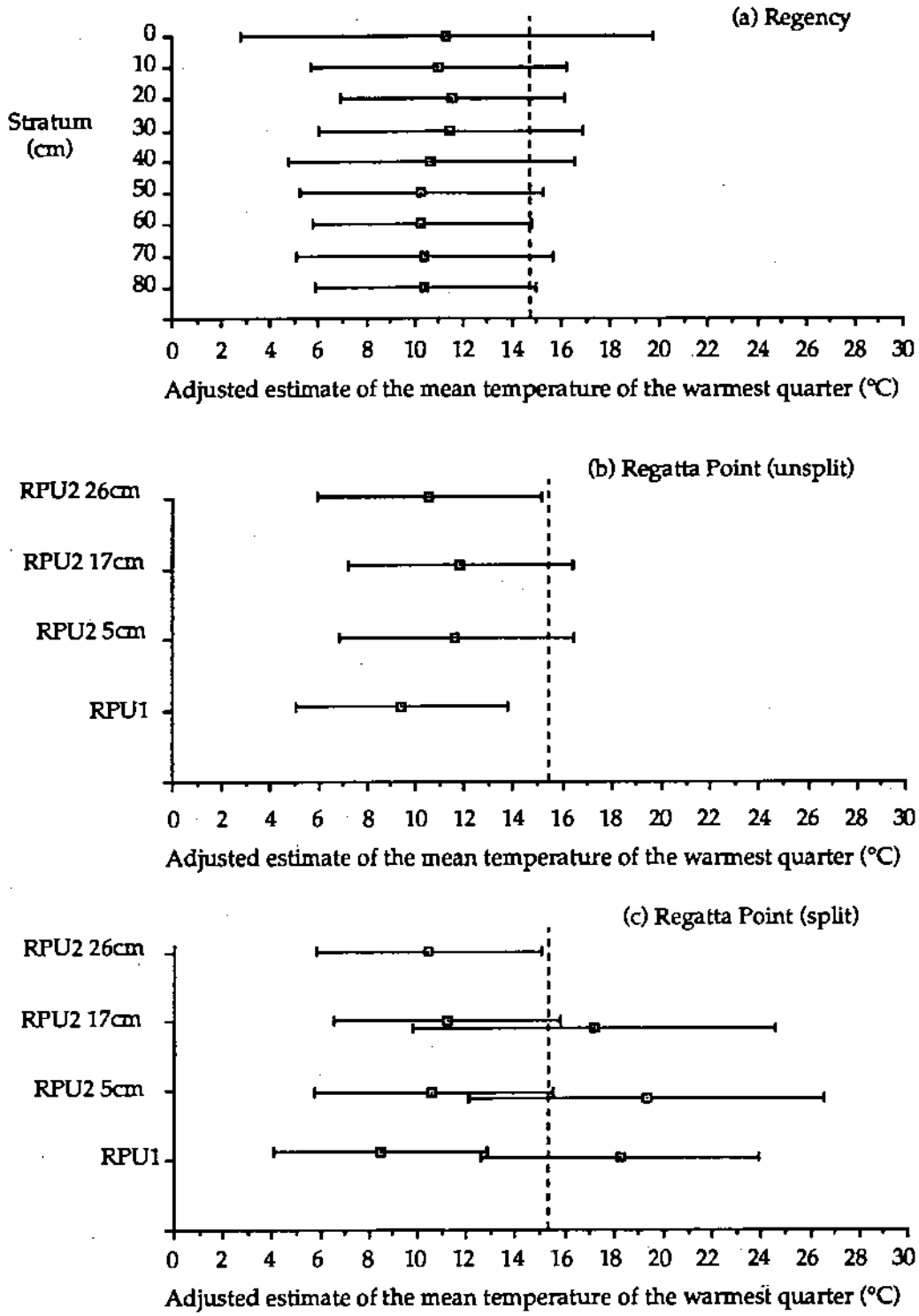


Figure 5.8 : Adjusted estimates of mean temperatures of the warmest quarter with 95% confidence intervals (bars) for source vegetation for fossil *Nothofagus cunninghamii*. These estimates and confidence intervals are derived from the regression analysis (see text) and are adjusted to allow for taphonomic effects (see text). The dashed lines are the BIOCLIM estimates of the current mean temperature of the warmest quarter for the sites. (a) Estimates from fossils from the Regency Formation separated into 10 cm layers (see chapter 2). The oldest samples are at the base. (b) Estimates from fossils from the Regatta Point sediments. (c) Estimates from the Regatta Point samples assuming that some of the samples are derived from more than one population (see text and Figure 5.6). Note the increasing overlap in confidence intervals from RPU1 through to RPU2 17 cm.

the warmest quarter, and in the Regatta Point samples the confidence intervals of two of the samples (RPU2 26 cm, and RPU1) do not reach the modern levels.

Figure 5.8 c shows the estimates and confidence intervals derived if the bimodality of the RPU samples is assumed to be evidence of two population sources. In each sample, the confidence intervals overlap. The overlap in the RPU1 sample is very narrow. If the bimodality is due to the local presence of two populations of *N. cunninghamii* then the region of overlap is the best estimate of temperature of the warmest quarter at the time of deposition for these samples. If, however, the bimodality is a taphonomic artefact then the results shown in Figure 5.8 b give the best estimates. Both interpretations have overlapping confidence intervals and trends are therefore ambiguous, but both show higher mean predicted temperatures for the RPU2 samples than the RPU1 sample. In either case, the RPU1 site is likely to have been cooler than it is now, perhaps by about 3° C, and the RPU2 site was likely to have been no warmer than it is now at Regatta Point.

5.4 : Discussion

The broad confidence intervals around the estimates shown in Table 5.2 and Figure 5.8 imply that this method is of limited use in predicting palaeotemperatures except in the special case discussed for Regatta Point. This variation is likely to be derived from several sources. One is sampling error, where the samples or subsamples are not representative of the population. Another is the effect of other environmental variables on leaf morphology. Historical effects are also likely to be important, where the plants are adapted to past rather than present local conditions. Chance variation may also play a part. Inaccuracies in the BIOCLIM estimates, particularly due to microclimate effects are another source of inaccuracy. The BIOCLIM estimates do not compensate for local effects of cool air drainage and aspect. These are particularly important for marginal populations of *N. cunninghamii* since these tend to occur in regions of favourable microclimate, e.g. south-east facing gullies in drier areas.

It is likely that similar uncertainty would become apparent in other methods of palaeoclimatic estimation using physiognomy if any rigorous attempts were made to place confidence intervals on them. The consequences may be less serious in some studies of Tertiary sites than here, because the desired degree of resolution required in these Quaternary studies is higher. However, uncertainties of the order of ±3-5 °C or more, implied in these estimates, are likely to apply to Tertiary physiognomic studies, and these are likely to invalidate the conclusions of some previous studies. A pertinent case of an analogous problem is that of Markgraf *et al.* (1986). This study predicted palaeoclimates for Holocene Tasmania based on proportions of pollen taxa. It failed to produce confidence intervals on their estimates, and assumed equilibrium conditions for modern vegetation, which largely invalidates their results. There are, however, a number of other significant implications of these results discussed below.

5.4.1 : Regency

The mean of log transformed leaf lengths of *N. cunninghamii* and, hence, the temperature estimates from Regency show only small changes (Figures 5.8 and 5.9) between the strata. The floristics of the site indicate a change in climate probably occurred during the period between the deposition of the material at 50 cm and the deposition of the 30 cm material. The mean leaf sizes from ≥50 cm depth are all smaller than all the mean leaf sizes from ≤30 cm depth, and the leaves from 40 cm are intermediate. A two stratum analysis of variance of log leaf lengths of the strata nested within the periods (≥50 cm, 40 cm and ≤30 cm) showed that the probability of the log transformed leaf lengths from 50 cm and before being the same as the log transformed leaf lengths of 30 cm and after was less than 0.0001. The leaves from 40 cm were not significantly different to either of the other periods. This is unlikely to be the result of differences in taphonomy, since very well preserved, well preserved and poorly preserved strata each occur both above and below the 40 cm stratum. This clear association of change in leaf form with a substantial change in floristics shows that leaf morphology does respond within sites to external environmental changes.

The estimates derived from the leaf morphometry do not, however, indicate any significant change in temperature even large climate would be necessary to induce such a change in floristics. The leaf morphometry is only linked here to temperature of the warmest quarter, but temperature and precipitation are closely linked in most climatic models for the Quaternary (e.g. Bowler 1982).

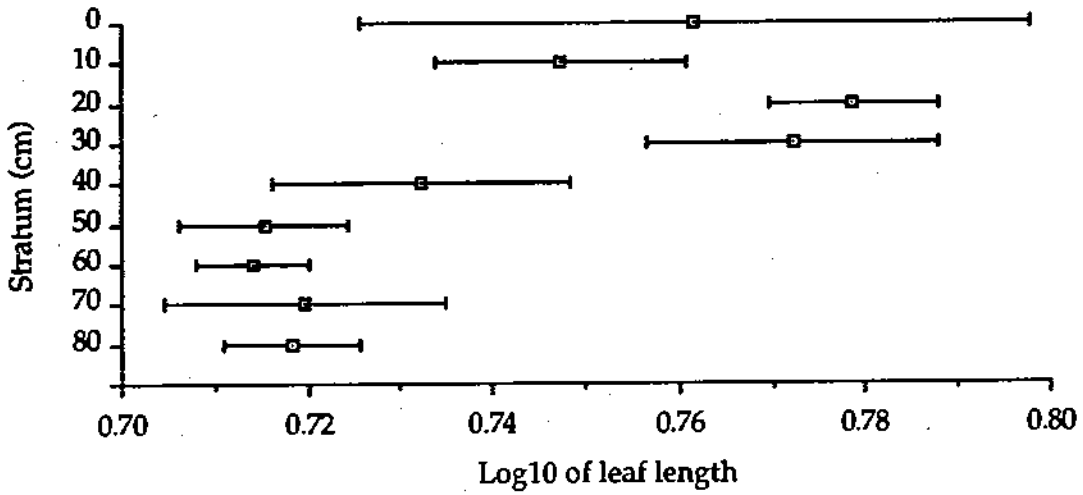


Figure 5.9 : Plot of means of log transformed leaf lengths of fossil *N. cunninghamii* from the different layers from the Regency Formation. The error bars are standard errors. Note the consistently lower values for the four lower samples than for the four upper samples, the intermediate value of the 40 cm sample. The 0 cm sample was poorly preserved, and contained only 10 leaves, so it has large error bars.

As discussed above, the changes in floristics (and hence leaf form) were likely to have been caused by climatic amelioration : increased temperature and precipitation. Some of the changes in floristics cannot be explained by increased precipitation (the losses of *Athrotaxis* and of *Microstrobos niphophilus* and the replacement of *Eucryphia milliganii* by *E. lucida*). It is highly likely that increased temperatures were involved. It is unlikely that a change in winter temperatures of sufficient magnitude to cause these changes in floristics could have occurred without a substantial change in summer temperature.

This conflict between the estimates of temperature from morphometrics and from floristics may be the result of a relative lag in the response of leaf size to climate change, the result of a relative lag in the response of floristics to climate change, or because the cause of the floristic change had

little effect on leaf length. The third explanation is unlikely since the main apparent causes of the change in floristics (increased temperature) is the main apparent cause in the change in leaf form.

There is likely to have been a significant lag in the response of leaf length to climate change. This will be greatest if the variation in leaf size between populations is derived primarily from genetic sources, rather than from phenotypic plasticity within genotypes, and if the diversity of the gene pool within populations is relatively limited. The lack of phenotypic plasticity within genotypes is supported by observations that glasshouse grown *N. cunninghamii* show only slight increases in leaf size or changes in shape from field grown plants, even though conditions differ greatly in the glasshouse from those in the field (Hill and Reid 1987). Less is known about the genetic diversity within extant populations, but leaf morphology does not generally appear to vary greatly between trees within populations. Under these circumstances, significant change in morphology in response to climate change is most likely to be derived from replacement of genotypes by others from regions of more suitable climate through seed or pollen dispersal and subsequent selection. The slowness of this change may well lead to a lag in morphological response.

Lag in the response of floristics to climate change is also likely. A significant lag will occur before new genotypes or species invade, since these introductions require dispersal events, and the availability of suitable sites for establishment. Where the floristic response is primarily the local extinction of taxa, as appears to have happened at Regency, this lag does not need to be so great. The loss of species is most likely to be due to an inability to regenerate effectively. This is especially likely in the case of the Regency sediments where the inductive change appears to be a climatic amelioration, and the floristic changes involve the loss of tree taxa. Tree taxa are relatively unlikely to die under warmer, wetter conditions but their seedlings may have considerable problems. Hence, the lag may be a few hundred years, or perhaps a few thousand years for very long lived taxa such as *Athrotaxis*. It is worth noting that the loss of *Athrotaxis* and *Microstrobos* (local extinctions) predated the replacement of *Eucryphia milliganii* by *E. lucida*. The small change in leaf morphology appears to

have occurred during the period between the time of the local extinction of *Athrotaxis* and *Microstrobos* and the time of the replacement of *E. milliganii* by *E. lucida*, and hence is probably a relatively rapid response.

The morphological response of *N. cunninghamii* to the climate change was small. This supports the hypothesis that major changes in leaf morphology lagged behind changes in floristics at this site. The small but significant changes are likely to be the Regency population of *N. cunninghamii* responding to the climatic amelioration within the bounds of the limited available genetic and phenetic plasticity. Later morphological adjustment through imported genetic material (seeds or pollen) may have occurred but this is not recorded in the fossil record.

An alternative hypothesis is that sufficient genetic variation occurs within populations to allow for responses to climate differences, that most of this variation is selected against under any given set of climatic conditions and new sets of conditions lead to selection of a different phenotype. The response to climate change could then occur within a few generations. However, this hypothesis is highly unlikely, firstly, because such genotypic variation is not apparent in informal glasshouse trials and, secondly, because it requires strong selection which would eliminate the variation relatively quickly.

An important corollary of significant lag in *Nothofagus* leaf morphology to climate change is that much of the variation between extant populations of *N. cunninghamii* is the result of historical effects. Hence, the leaf morphology of extant populations should contain considerable information about the history of these populations.

This historical effect has important consequences for the validity of the climatic estimates made from correlation of extant leaf morphology with extant climates. A clear example of probable historical effects can be seen in the log transformed leaf lengths of *N. moorei*. There is virtually no difference in the means of the log transformed leaf lengths between any of the populations measured in this study although these populations exist under a wide range of climates (Figure 5.7). This species does not vary in response to climate in the normal way for most species. This is most likely to be the result of the species having limited genetic variability, due to some

aspects of its Quaternary history.

The importance of historical effects in determining the leaf size of populations of *N. cunninghamii* has consequences for the climatic estimates made by correlation of the leaf size of modern populations with modern climates. Global climate shifts will affect all populations. Hence, most populations are likely to have leaf lengths which are shorter than the climatic optimum after recent increases in temperature, and longer after recent decreases in temperature. The climate over the last 17,000 years has included a large increase in temperatures until about 9,000 years ago, and probably a slight decrease in temperatures since about 5,000-6,000 years ago (e.g. Shackleton and Opdyke 1973). The Regency data seem to suggest that the lag time for major responses in leaf morphology are quite large (probably in the order of thousands or tens of thousands of years), so it is unclear whether modern *N. cunninghamii* leaf morphology reflects glacial or interglacial conditions. Hence, in addition to taphonomic biases there are two sources of bias in the estimates. One is the bias in the extant leaf morphology due to the Late Last Glacial and Holocene climate history, and the other is the bias in the fossil leaf morphology due to the climatic history preceding the time of deposition. These biases are particularly relevant to studies of Quaternary deposits because of the volatility of the climate during this period. A significant part of the effects of these biases should be compensated by the confidence intervals around the estimates. As argued above the bulk of the variation between sites appears to be the result of historical effects. It is assumed that the divergence from optimum leaf form in the past is not significantly greater than at present, except where there was a rapid and large change in climate (of, say, 3 or 4 °C or more in less than 1000 years). Such changes apparently only occur at the end of glacials and should be apparent from other evidence in the sediments. Under the assumption of similar divergence from optimum in the past as occurs at present the confidence intervals around the estimates should include the true palaeotemperatures.

The estimates of mean temperature of the warmest quarter shown in Figure 5.8(a) are not inconsistent with the floristics. They give estimates generally lower than current conditions, but the current mean temperature

of the warmest quarter falls within the confidence intervals. As discussed above there is likely to be an ecological lag involved here, so the estimates are likely to be underestimates, but the real palaeotemperature is likely to lie within the confidence intervals. Hence, there is no evidence from the leaf form of *N. cunninghamii* of significant divergence from current temperature conditions during the Regency Interglacial.

5.4.2 : Regatta Point sediments

The *Nothofagus* from the RPU1 sample is consistent with a derivation from the equivalents of two extant *N. cunninghamii* populations of considerably different leaf size and highly inconsistent with being derived from the equivalent of one extant population. These two populations are one consistent with ones adapted to cold (almost alpine) conditions, and the other consistent with adaptation to conditions as warm as, or warmer than, at present (Figure 5.8).The RPU2 samples appear to form a continuum from thee 5-6 cm sample which approaches the RPU1 sample in bimodality to the 26-27 cm sample which is consistent with a derivation from two populations of similar leaf size, or a single population which is more variable than extant populations of *N. cunninghamii*. Collections of *N. cunninghamii* leaves extracted from small samples from different layers of the sediments show an unusually wide range of sizes (by comparison with modern samples), and the RPU2 samples indicate that a bimodal distribution and large variance of leaf lengths is likely, so the distribution shown by the RPU1 sample is assumed not to be the result of its composite nature. The Early Pleistocene was of the order of 1 million years long, so the palynological dating allows for considerable temporal differences between the RPU2 and RPU1 sediments. However, there are several reasons to suggest that the blocks do not differ greatly in age. Macrofossils of now extinct taxa which are unknown anywhere else (*Rubus* sp., *Banksia strahanensis*, *Oxylobium* sp. and *Proteaceae* genus unknown #1) occur in both RPU1 and RPU2, and both sets of sediments have similar forms of extant taxa which differ significantly from modern forms, e.g. *Eucryphia* sp., *Athrotaxis* cf. *laxifolia* and *Telopea* cf. *mongaensis* . There is no evidence of extensive areas of Early Quaternary macrofossil bearing sediments in this

area, and it is unlikely that they ever existed. It is highly unlikely that the blocks were transported any great distance, so the co-occurrence of restricted areas of macrofossil bearing sediments of significantly different ages is unlikely. The co-occurrence of the Eocene and Pleistocene sediments is a less unlikely event since the fossiliferous Eocene sediments cover a large area (hundred of square kilometres). Finally, the bimodal distribution of *N. cunninghamii* is an unusual event, unless it is the result of the presence of two otherwise cryptic species, which is unlikely for the reasons discussed below. It is therefore unlikely that the conditions which gave rise to this situation arose independently on separate occasions in the same place.

Populations of *Nothofagus cunninghamii* may have been far more variable than they are now, and the bimodal distribution of leaf lengths may be the result of some unknown taphonomic bias. This is unlikely since taphonomic biases normally favour either smaller or larger leaves but not both, and none of the extant sediment samples show any indication of such a bias.

Two species of *Nothofagus* similar to *N. cunninghamii* may have co-occurred in the locality. This implies a degree of genetic isolation of the forms, due to reduced fitness of hybrids, or less likely due to extreme rarity of hybrids due to phenology. The ordering of the ages of the sediments consistent with this hypothesis would be that the RPU2 sediments were older than the RPU1 sediments and, within the RPU2 sediments, the top of the block (26 cm) were older than the bottom of the block, then the sequence shows a clear splitting of the *N. cunninghamii* into two groups. However, within a site this is highly unlikely to occur except by sympatric speciation. It is highly unlikely that any fossil site would include such a continuous record of speciation, and this possibility cannot be accepted while other reasonable explanations are available. This ordering of ages would be superficially consistent with stepwise extinction from RPU2 to RPU1. As noted in Chapter 2, however, there are no palynological differences between the two sites considered to be of stratigraphic importance, and therefore, the higher proportion of apparently mesic, now extinct taxa in RPU2 is not strong evidence of an older age than RPU1.

If, on the other hand, the RPU1 material is older than the RPU2 material then the data may be explained as being the result of the mixing of two populations of *N. cunninghamii*. Mixing of taxa is likely to occur after major climatic change, for example at the beginning of an interglacial. A model is therefore proposed where RPU2 is older than RPU1 and both are early in an interglacial. The presence of apparently more sclerophyllous vegetation in RPU1 than in RPU2, with a higher proportion of *Allocasuarina*, is consistent with this hypothesis, since this appears to be normal early in an interglacial (see chapter 2). The presence of a higher proportion of mesic taxa in the RPU2 sediments may merely represent the expansion of these taxa after restriction by the cold and dry conditions during a glaciation of upland areas. This is also consistent with this hypothesis in light of the results of the leaf morphometrics of the Regency *N. cunninghamii*. There, leaf size appeared to lag behind changes in floristics with increasing temperatures. General floristic changes in the source vegetation of the Regatta Point sediments appear to have occurred before the apparent mixing of populations of *N. cunninghamii*.

The implications of ecological lag in Tasmanian ecology, and of the apparent mixing of two forms of *N. cunninghamii* are discussed in Chapter 7.

Chapter 6 : Extinction and Diversity Changes in western Tasmania

6.1 : Introduction

Extinctions of plants, animals and presumably other groups of living things have occurred throughout the long history of life on Earth. Most species that have ever lived are extinct (Raup 1991). Extinctions can be classified as local, regional or global, and by taxonomic level (e.g. of subspecies, species, genus or family). Local and regional extinctions represent changes in the distribution of taxa. Rates of extinction have apparently varied greatly throughout history (e.g. Raup 1991).

Mass animal extinctions have occurred at the Permian/Triassic and Cretaceous/Tertiary boundaries, and at other times (e.g. Raup 1991). There remains controversy as to whether similar catastrophic extinctions have occurred among land plants. There have been periods of high levels of extinction, but Knoll (1984) and Hickey (1984) argue that these tended to extend over thousands and millions of years and often appear to be related to climatic changes, rather than a period of no more than a few years as appears to be the case with animals in the terminal Cretaceous event. In contrast, Johnson (Johnson *et al.* 1989; Johnson and Hickey 1990) show a disproportionately high number of plant species extinctions at the Cretaceous/Tertiary boundary in western U.S.A. Knoll (1984) proposed that plant groups are less prone to catastrophic extinction than animals because they differ from animals in ways that determine the nature of extinction :

(1) plant species are more prone to extinction from competition than animals, since plants are, in general, competing for the same resources : light, water and soil borne mineral nutrients, whereas animals may have the option of switching resources (niche displacement),

(2) plant species are more prone to extinction from climate changes, since the current distributions of plants generally reflect climatic conditions more closely than animals, and

(3) plants are more resistant to catastrophic short term disruptions, since they are sedentary. Vascular plants are almost all fixed to one substrate or another, so they have evolved ways of tolerating stressful periods, such as broad ecological tolerance or ways of regenerating after

major disruptions, e.g. soil seed storage and vegetative reproduction. Animals are more likely to respond to disturbance by moving. If the disturbance is too widespread to flee, animals are less likely to leave viable propagules.

Worldwide, both micro- and macrofossils indicate many regional extinctions of plant groups in the Late Cainozoic, but there is very little evidence of global extinction. The clearest evidence of late Cainozoic global extinctions comes from macrofossil evidence. Leopold (1967) used seed floras of northern Europe, and elsewhere, to show that most late Cainozoic extinctions had occurred by the end of the Tertiary, and the few now extinct species almost all disappeared from the fossil record early in the Pleistocene. There are, however, few studies of leaf fossil floras from the Early-Middle Pleistocene.

Oliver (1928) describes leaves and fruit from sediments in the North Island of New Zealand, and considered many of these to be from extinct species. Couper and McQueen (1954) suggest that these sediments are probably Early Pleistocene. The determinations of these taxa are not strong since they are based solely on 'picture matching' of venation and leaf shape, and the dating of the sediments is uncertain. The significance of these fossils is, therefore, unclear but re-examination of these fossils may be of considerable interest. Therefore, the evidence for plant extinction in the Late Cainozoic is sparse.

Apart from the new evidence presented in this thesis there is little evidence of the global extinction of any plant taxon present in Tasmania, or indeed, in Australia in the Late Cainozoic. Many extinctions may not be apparent in the fossil record probably because virtually all Pliocene and Early Pleistocene studies are based on microfossils. Pollen of Casuarinaceae larger than known forms occur in the Lake George sediments from the Middle and first part of the Late Pleistocene(Singh *et al.* 1981). It is likely that this represents the extinction of a species, or group of species, since the loss of this pollen type coincides with the increase in charcoal in sediments, and the apparent replacement of Casuarinaceae by *Eucalyptus* as dominants of sclerophyll vegetation (see Chapter 7). Kershaw (1984) suggests that there have been few extinctions of major

plant taxa, and few extinctions at any level in the Late Cainozoic due to plants' ability to survive in refugia, slow evolutionary rates and a trend to increasing diversity rather than replacement of species. There is evidence of regional extinction of some taxa in this period.

The Late Tertiary and Early Pleistocene is believed to have been a period of progressive reduction of rainforest in Australia in response to a broad climatic trend towards cooling and drying (Kershaw 1988). Tasmania appears to have followed these trends, although rainforest types may have persisted there longer than on mainland Australia. Table 6.1 summarizes the occurrence of pollen types now extinct from Tasmania, which are known from Pleistocene sediments in Tasmania (Hill and Macphail 1985; Fitzsimons *et al.* 1990; M. K. Macphail pers. comm.). Several pollen types which can be reliably assigned to groups now extinct from Tasmania have been found in the Linda Valley sediments, which are latest Pliocene to earliest Pleistocene in age (Hill and Macphail in press, see chapter 2). The conifer taxa Araucariaceae, *Dacrycarpus* and *Dacrydium*, and Angiosperm taxa *Beauprea*, *Ascarina*, *Quintinia* and *Nothofagus* subgenus *Brassospora* have sufficiently distinctive pollen types to represent clear regional extinctions (Hill and Macphail in press). The presence of each of these taxa is not likely to be the result of reworking or long distance transport, since they are common and well preserved (M. K. Macphail pers. comm.). Araucariaceae is restricted to subtropical and tropical regions in Australia, New Guinea and the South Pacific, but also occurs in montane temperate areas of South America. *Dacrycarpus* and *Dacrydium sensu stricto* are extinct from Australia, but occur in cool and warm temperate forest in New Zealand, and in tropical and subtropical areas elsewhere in the southern Hemisphere. *Beauprea* is now endemic to New Caledonia. *Ascarina* is extinct from Australia and now occurs in cool temperate New Zealand, and elsewhere. *Quintinia* occurs on mainland Australia in warm temperate, sub -tropical and tropical forests, and also occurs in cool temperate forests in New Zealand. *Nothofagus* subgenus *Brassospora* now only occurs in New Guinea and New Caledonia. Most of these pollen types are common in Tertiary sediments in Tasmania (Macphail *et al.* in press), and macrofossils of many of these groups are known from Tasmanian Tertiary sediments

Taxon	Linda Valley	RPU2	RPU1	Darwin Crater (near base)	Regency	Late Pleistocene
Quintinia	+	+	+	+	+	+
Gothanipollis perplexus (Loranthaeae)		+	+	+	+	
Stephanocolpites oblatus	+	+	+	+		
Nothofagus subg. *Brassospora*	abundant	+	+			
Banksia sp.		+	+			
Dacrycarpus	+	?	+			
Lagarostrobos sp.	+	+	?			
Dacrydium	abundant	+				
(?)*Pseudanthus*	+	?				
(?)*Austrobuxus*	+	?				
Myrtoideae	>1 species	+				
Asteraceae sp.	+	+				
Symplocos		+				
Araucariaceae	+					
Ascarina	+					
Other Podocarpaceae (3 spp.)	+					
(?) Arecaceae	+					
Eucalyptus sp.	+					
Beauprea	+					
Stylidiaceae sp.	+					
Droseraceae sp.	+					
Liliaceae sp.	+					

Table 6.1 : Known occurrences in Late Pliocene and Pleistocene sediments in Tasmania of pollen of taxa which are now extinct. The ages of the sediments are : Linda Valley is Late Pliocene-Earliest Pleistocene, RPU1&2 are Early Pleistocene, Regency is probably Middle Pleistocene and the part of the Darwin Crater containing *Gothanipollis* is Middle Pleistocene (about 600,000 B.P.).

(Carpenter *et al.* in press), and so their presence is inferred to be the result of persistence of elements of the Tertiary vegetation.

The Early Pleistocene Regatta Point sediments contain pollen of fewer now extinct taxa than the Linda Valley sediments. Most of these extinct taxa are also known from the Linda Valley sediments. The RPU1 sediments also contain trace levels of several taxa which are not known elsewhere in sediments from south-east Australia younger than Miocene and it is likely that there has been some reworking from the abundant local Early Tertiary sediments (Hill and Macphail 1985). *Gothanipollis perplexus* and *Quintinia* pollen occur in the Early to Middle Pleistocene Regency Interglacial sequence (Fitzsimons *et al.* 1990). *Gothanipollis perplexus* and *Stephanocolpites oblatus* (a 'Tertiary' taxon of unknown affinity) occur near the base of the Darwin Crater core (probably about 600,000 B.P.) (M. K. Macphail pers. comm.). Trace levels of *Quintinia* pollen persist into the Late Pleistocene (Fitzsimons *et al.* 1990; E. A. Colhoun pers. comm.). *Gothanipollis perplexus* is a pollen species derived from the Loranthaceae, and therefore probably from a wet forest parasite species.

The microfossil record therefore shows a trend of decreasing occurrence of regionally extinct 'Tertiary' wet forest taxa from the end of the Tertiary to the Late Pleistocene. Most of these are last recorded in the Linda Valley sediments, somewhere near the Pliocene-Pleistocene boundary. A few persist until the time of deposition of the Regatta Point sediments. Only two are known to occur after the most extensive glaciation (the Linda Glaciation), although it is not clear whether the Regatta Point sediments were deposited before or after this glaciation.

There is some evidence of local extinction, e.g. *Sambucus gaudichaudiana* pollen and *Cyathea* spores occur in Late Pleistocene sediments from Melaleuca Inlet in far south-western Tasmania, but in Tasmania *S. gaudichaudiana* is now restricted to drier areas of Northern Tasmania and *Cyathea* is now restricted to the north-east and some isolated populations in the south-east and west (Jordan *et al.* 1991).

Extinctions are individual events, which may occur singly (isolated extinctions) or many may occur at the same time, in the same area (multiple extinctions). Isolated extinctions are usually considered to occur more or less continuously, and may be the result of internal causes, such as

competition. These are sometimes called 'normal' extinctions (e.g. Diamond 1984). Large changes in regional diversity require multiple extinctions. Multiple extinctions may be the result of close ecological relationships (e.g. a parasite dependant on a single host will become extinct if the host does), coincidence, or of some major environmental change. Multiple extinctions due to coincidence are only likely to involve a few species, even when considered over the geological time scale, and hence will not have a significant effect on diversity. Multiple extinctions due to the normal extinction of a species followed by the extinction of other ecologically interrelated species are also unlikely to involve more than a few species, although there is evidence of the existence of 'keystone' species upon which whole groups of other organisms are largely dependant (e.g. Paine 1966). Roughgarden (1979) suggests that many animal top predators may act as keystone species. How this applies to plants is less clear. It is possible that the effects of major disturbance and close ecological relationships act together to exacerbate extinction events (i.e. environmental disturbance may directly cause the extinction of some species, and other species which have close ecological relationships with extinct species may secondarily die out) (e.g. Jablonski 1991). Hence, multiple extinctions associated with significant changes in diversity are good evidence of some strong cause for extinction : most likely an extrinsic environmental change, but possibly the normal extinction of a keystone species. It is, therefore, useful to consider changes in diversity when discussing extinction during the Quaternary.

Diversity is a complicated issue. It may be composed of diversity within species (the size of gene pools), the number of species (species diversity) or the number of higher order taxa present (disparity *sensu* Gould 1989). The discussion of diversity presented here will be primarily concerned with species diversity, since this is the most easily measured aspect of diversity, but diversity within species will also be considered. Comparisons of species diversity can be made in two ways : one is to discuss the presence or absence of individual taxa within each of the communities to be considered (qualitative analysis). The other is to count the number of specimens of each taxon in samples from each community and to use statistical methods to make comparisons between them (quantitative analysis).

The relationship of expected number of species versus subsample size expresses the species diversity of a sample. The diversity of the

sediments can then be estimated from these samples by the use of replicates, or where replicates are not available (as in most of the sites here) by assuming that the sample is more or less typical of the site, and the variation within the site is similar to that within the sites with replicates (where there is an estimate of the variation). The diversity of the source vegetation can then be inferred from the diversity of the sediments if the effects of taphonomic processes are taken into account. Hence, estimates can be made of the diversity of source vegetation from sediment samples, but a number of assumptions are made in this process and these need to be explained and justified. This logical process also applies to qualitative analyses.

This chapter summarizes the evidence for Quaternary plant extinctions and tests the hypothesis (implicit in Brown and Kirkpatrick 1984) that the diversity of plant communities has changed during the Quaternary. This hypothesis is tested using the presence of macrofossils of now extinct and now extant species in the RPU1 & 2, Regency and Melaleuca Inlet sediments. Rarefaction methods are used to assess the overall diversity of woody plant species in the catchments of the fossil sediments and compares them with modern equivalents. Qualitative methods are used to assess the diversity of lowland rainforest in western Tasmania past and present. The nature of some of the extinctions are then discussed.

6.2 : Materials and Methods

The following large samples were included in the quantitative analysis of diversity :

(1) Little Rapid River (Early-Middle Oligocene (Hill & Macphail in press)). Carpenter *et al.* (in press) propose that this site had high plant diversity and the overall diversity of rainforests was significantly higher in Tasmania during the Tertiary than it is now, although parts (particularly the Paleocene, Middle and Late Miocene and Pliocene) are largely unknown.

(2-4) Each of the three main leaf beds of RPU2. Each of these layers is likely to have been deposited in a short period (see chapter 2), and therefore these sediments should be comparable with surface sediments from modern lake bottoms.

(5) A pooled sample from other blocks at Regatta Point. The other blocks were those studied by Hill and Macphail (1985) and other floristically similar blocks.

(6-11) Each of the ten centimeter sections of the Regency [Early-Middle Pleistocene (Fitzsimons *et al.* 1990)] core which contained more than 600 leaves (at 20 cm, 30 cm, 50 cm, 60 cm, 70 cm and 80 cm).

(12) The leaf samples collected from the Melaleuca Inlet sediments.

(13-19) Seven samples of sediments from the base of Lake Dobson randomly chosen from those samples collected by Hill and Gibson (1986 a) which contained more than 600 leaves (see chapters 2, 4 & 5).

(20-22) Three samples collected from Hastings Pool (see chapters 2, 4 & 5).

(23&24) The samples collected from the banks of the Old River and Melaleuca Creek (see chapters 2, 4 & 5). This vegetation is diverse, but probably less so than around Lake Dobson.

The first 12 samples are fossil sites, and the last 12 sites are extant samples of leaf deposits for comparison. R. S. Hill provided the data for the Little Rapid River, and Lake Dobson sites. In each case, all identifiable leaves and leaf fragments were identified and included in the analysis. All the fossil floras are of mummified leaves in fine grained sediments.

6.2.1 : Statistical Methods

Estimates of the expected number of species in a subsample of given size from each large sample were made with a program written in SAS (SAS Institute Inc. 1988 a&b). This program counts the number of species in many random subsamples of given size from the number of each species in the large sample. 28 random sub-samples of 128 leaves were made from each large sample. Means of the number of species per random subsample will be referred to here as the expected numbers of species. This method is rarefaction by repeated subsampling, as suggested by Simberloff (1979) as an alternative method to explicit calculation, and is analogous to the bootstrap method and makes few assumptions about the relationship between species and sample size. Rarefaction has been used in the analysis of diversity of fossil assemblages in several different ways (e.g.

Raup 1975; Birks and Line 1992; Foote 1992). Most studies have used the exact algorithms of Hurlbert (1971) and Heck *et al.* (1975) to calculate expected numbers and variances. Foote (1992), however, used rarefaction by repeated random subsampling.

The method of rarefaction is distribution free. Other commonly used methods of assessing the relationship between sample size and number of species invalidly assume that this relationship follows a given form of curve (log-linear, or power relation) (Connor and McCoy 1979). Sanders (1968) explained the conditions required for comparisons to be made between different samples by rarefaction :

(1) the samples need to be taxonomically similar

(2) sampling methods need to be consistent

(3) the samples should be from similar habitats and

(4) the method can only be used for interpolation. Extrapolation can be used where a regression model has been justified and fitted, i.e. where an underlying model is assumed.

To these can be added the assumption that the taxa are randomly distributed within the sample (Simberloff 1979). The samples used in this study satisfy these conditions except there are discrepancies in the sampling methods (see discussion). It is assumed that the diversity of fossil and extant samples can be compared and this relates indirectly to the diversity of source vegetation (see discussion).

The numbers of species in the random subsamples did not satisfy the conditions of analysis of variance, so all the estimates were placed in rank order and assigned rank scores which allowed the data set to meet these assumptions. Means of these ranks were compared using the Ryan Einot Gabriel Welch multiple range test (REGWQ) after one way analysis of variance. REGWQ was chosen to test the differences since it is a powerful test which permits the simultaneous testing of means, providing the number of observations per treatment is constant and the variances of different treatments are approximately equal (SAS Institute Inc. 1988 c). This tests whether the samples have different diversities, but does not test whether the sediments differ (for which the use of replicate samples is best).

Replicate samples were available at four sites : RPU2, Regency, Lake

Dobson and Hastings Pool. One way analysis of variance using the expected number of species found in subsamples of 128 leaves was used to compare the diversity of these sites. *A posteriori* comparisons were made between the means using Tukey's method. Tukey's method was chosen since it is a powerful method which is robust to differences in cell size (Day and Quinn 1989). The replicates from the extant sites, Hastings Pool and Lake Dobson, were samples from different positions within the depositional areas, and the replicates from the fossil sites, RPU2 and Regency, were samples of different age from the same places. The replicates from the fossil sites are therefore not strictly equivalent to the replicates within extant sites, and may reflect vegetation change through time rather than variation within the deposition site at one time. There are not, however, strong floristic differences between the strata of the fossil sites and the variances within the fossil sites are similar to those within the extant sites, so it is assumed that the two types of replicate are comparable.

Samples were rarefied to a range of subsample sizes in order to assess whether the sub-sample size of 128 was representative of the differences between samples. Eight random subsamples were generated at each of several subsample sizes (4,8,16,32,64 etc.) from each large sample. For each large sample, four plots were made:

(1) expected number of species against subsample size (i.e. number of leaves),

(2) log of expected number of species against subsample size,

(3) expected number of species against log of subsample size, and

(4) log of expected number of species against log of subsample size.

The best method of comparing the diversities of the samples would be to fit some regression to them. Connor and McCoy (1979), however, argued that there is no theoretical basis to establish the form of the relationship between species number and sample size, so regressions with any power to extrapolate cannot be fitted. The relationship between expected number of species and sample size is continuous and strictly increasing, and smooth curves are likely both inside and outside the constraints of the large sample size so some comparisons can be made between the trends shown in different samples.

Where the relationships were approximately linear it can be clearly seen if the lines from different samples cross, or appear likely to cross within reasonable sample sizes. If the lines cross, the relationship between rarefied estimates of number of species will be qualitatively different for different subsample sizes (e.g. at a small subsample size sample 1 has a higher expected number of species than sample 2, but at a larger subsample size sample 2 has a higher expected number of species). Where the relationships are approximately linear and divergent, differences at virtually any subsample size will the same (qualitatively) as the differences at any other size. In these cases, differences between rarefied subsamples will be good expressions of differences in species diversity. It is difficult or impossible to assess whether the lines will cross if the relationships between expected number of species and subsample size are curved. The greater the curvature, the more serious this problem. Quadratic curves were fitted to each of the relationships listed above to test for curvature. The quadratic component of these regressions is a conservative estimate of curvature. Where there is a significant quadratic component in these regressions there is evidence of curvature, and the size of the component is an estimate of the degree of curvature. There may, however, be curvature present when the quadratic component is not significant. A positive quadratic component means that the relationship is curved concave up, a negative quadratic component means concave down.

6.3 : Results

Species which occur as macrofossils in Quaternary sediments in Tasmania but are now extinct are listed in Table 6.2.

Table 6.3 shows the results of the analysis of variance of the expected number of species in 128 leaf subsamples between the sites with replicate samples. Figure 6.1 shows the expected number of species for each site.

Based on the sub-samples of 128 leaves, the Hastings Pool and Regency sediments have very low species diversities, and are exceeded by the Lake Dobson, which is exceeded by RPU2, assuming the samples represent the sediments as a whole. Since there are no replicate samples at the other sites, comparisons are only made between the samples rather

than the sites. The Little Rapid River sample has a relatively high diversity. The Old River sample has a relatively high diversity, similar to the RPU2 samples, higher than the Lake Dobson samples but lower than Little Rapid River. The diversity of the RPU1 sample is lower still, but at higher sample sizes it is likely to be similar to the Old River and RPU2 samples (i.e. the 128 leaf subsample is probably an underestimate). The Melaleuca Inlet sample is lower, similar to the less diverse Lake Dobson samples but higher than the Regency and Hastings Pool samples.

	RPU1	RPU2	Melaleuca Inlet
Globally Extinct taxa			
Banksia kingii			+
B. cf. *kingii*	+		
B. strahanensis	+	+	
* *Quintinia* sp.nov.	+	+	
* aff. *Dacrycarpus/Dacrydium*		+	
Oxylobium sp. nov.	+	+	
Acacia sp.nov.	+		
(?*) ? Proteaceae genus unknown #2		+	
Orites sp. nov.	+		
Taxa Extinct from Tasmania, and Probably Globally Extinct			
* aff. *Austromyrtus*	+		
Telopea cf. *mongaensis*	+	+	
* *Rubus* cf. *moorei* forma *glabra*	+	+	
(?*) Proteaceae genus unknown #1	+	+	
(?) ? *Anopterus* sp.	+		
(?*) *Callitris/Actinostrobus* sp.		+	
* *Laurophyllum* sp.		+	
Probably Extinct Taxa			
Allocasuarina cf. *verticillata*	+	+	
Athrotaxis cf. *laxifolia*	+	+	
Barbella cf. *nitens*		+	
Podocarpus cf. *lawrencii*	+		
Acradenia sp.	+		

Table 6.2 : Extinct taxa known as macrofossils from Quaternary sediments in Tasmania. The sites are described in Chapter 2. Taxa marked with an * are probable rainforest taxa which have no close relative in lowland rainforest in Tasmania.

SITE	Mean number of species	Probablity of equality with		
		L. Dobson	Regency	Hastings Pool
RPU2 (fossil)	16.66	p<.05	p<.001	p<.001
Lake Dobson	10.8	-	p<.001	p<.001
Regency	6.34	-	-	Not significant
Hastings Pool	3.7	-	-	-

Table 6.3. : Pairwise comparisons between the expected numbers of species in samples of 128 leaves from sites with replicated samples. Comparisons are made using Tukey's method after analysis of variance.

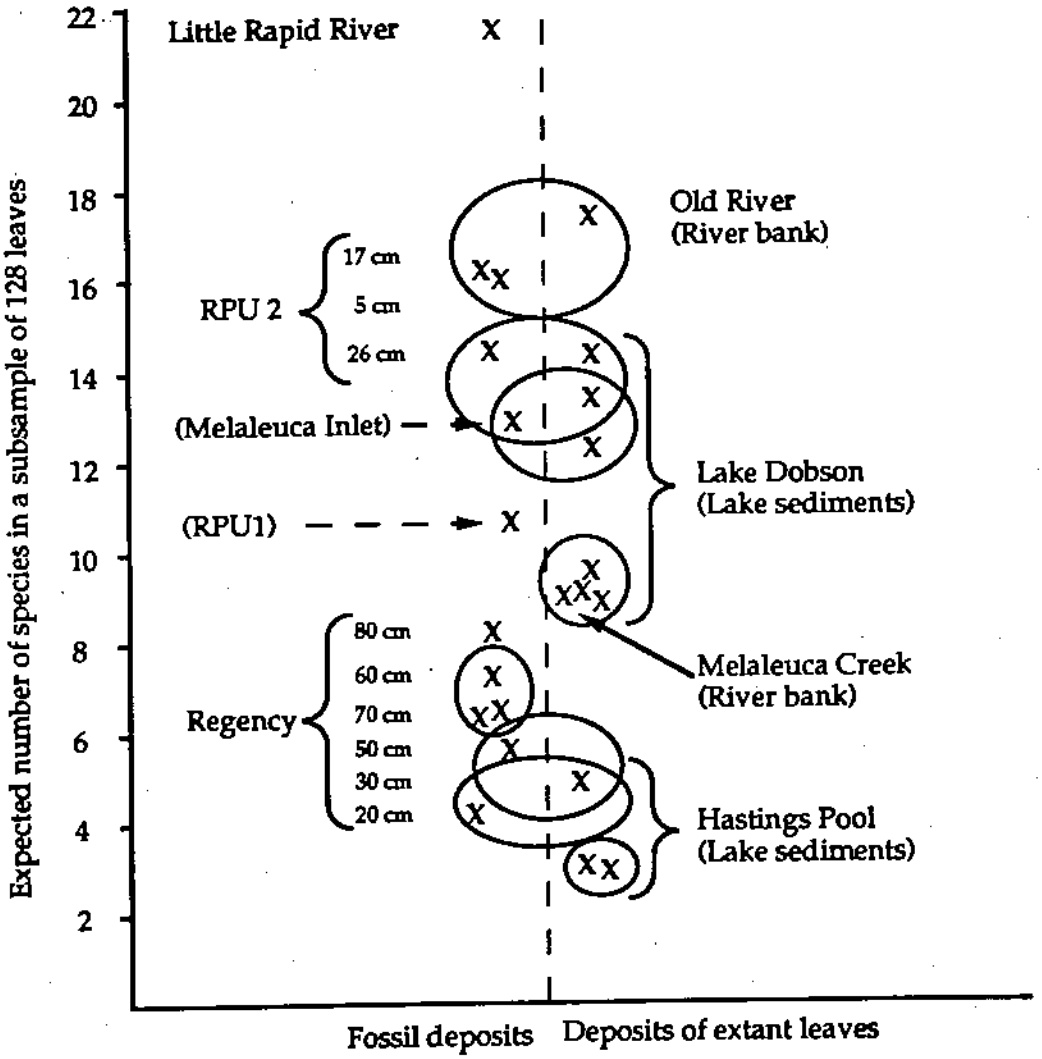


Figure 6.1 : Estimates of the expected number of species in a sub-sample of 128 leaves for fossil and extant sediment samples. Estimates enclosed in circles are not statistically significantly different from each other ($P \geq 0.05$).

Transformation	Numbers of regressions			
	Negative ($p<0.05$)	Negative (N.S.) ($p\geq0.05$)	Positive (N.S.) ($p\geq0.05$)	Positive ($p<0.05$)
None	17	6	0	0
Log(number of leaves)	0	9	6	8
Log : Log	16	6	1	0

Table 6.4 : Quadratic components of quadratic regressions of the samples listed in 'Methods' : numbers of components which are significantly positive, negative or not significant for different transformations. Under 'Transformation', 'None' means quadratic regressions of expected number of species versus subsample size; 'Log(number of leaves)' means quadratic regressions of expected number of species versus the logarithms of subsample size; 'Log : Log' means quadratic regressions of the logarithms of expected number of species versus the logarithms of subsample size. Numbers under 'Negative' are the numbers of regressions with significant, negative quadratic coefficients (at $p<0.05$); under Negative 'N.S.' are the numbers of regressions with negative but not significant quadratic components; under Positive 'N.S.' are the numbers of regressions with positive but not significant quadratic components; and under 'Positive' are the numbers of regressions with significant, positive quadratic coefficients (at $p<0.05$). Probabilities are based on two tailed tests.

Table 6.4 summarizes the quadratic components of the regressions of expected number of species against sub-sample size and two of the transformations of this relationship. The quadratric regressions of the logs of expected number of species against sub-sample size did not satisfy the normality criteria of the analysis, and are not considered further. More untransformed regressions (> twice as many) and log : log transformed regressions (twice as many) showed significant curvature than the regressions in which only sample size was log transformed. All the untransformed regressions, and all but one of the log : log transformed regressions were curved concave down. It is clear that there is a general cause of curvature in these relationships, which is likely to confuse the interpretation of the data. Rarefying one large sample containing over 28,000 leaves (all the Lake Dobson samples pooled together) showed very strong curvature of all these relationships except the untransformed number of species against log of number of leaves. This is in contrast to the results of Connor and McCoy (1979) for species/area relationships, and probably

implies that species/sample size relationship is simpler than the species/area relationship. It is inferred, therefore, that the relationship of expected number of species to the log of sub-sample size is less frequently, or less severely, curved than the other relationships, and will be used in the following discussions.

Figure 6.2 shows the relationship of expected number of species versus the subsample size for a representative selection of the large samples. Figure 6.3 shows this relationship for the RPU1 and RPU2 samples and the Old River sample. Figures 6.4 and 6.5 show this relationship for the Lake Dobson and Hastings Pool samples respectively.

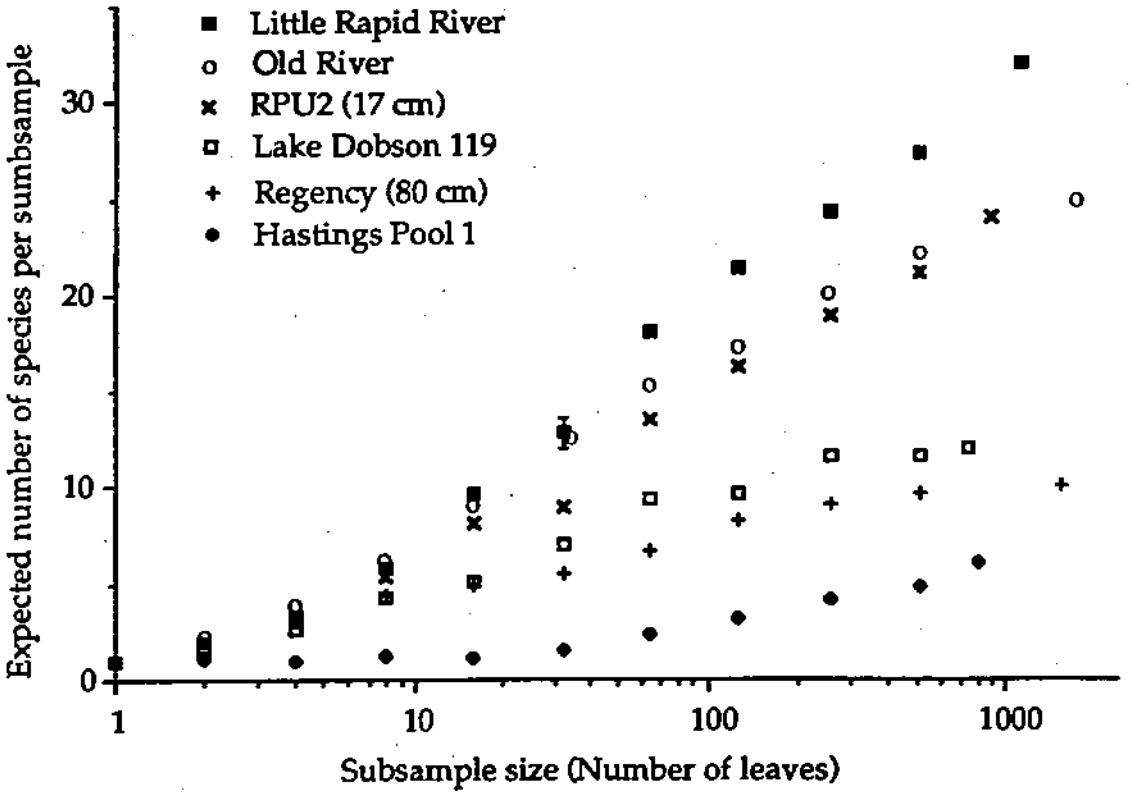


Figure 6.2 : Rarefaction curves of expected number of species *versus* number of leaves for some fossil samples, modern Lake sediments and river borne leaf sediments. Little Rapid River, RPU2 (17 cm), and Regency (80 cm) are fossil samples. Lake Dobson 119 and Hastings Pool 1 are modern lake bottom samples. Old River is a sample of litter from a river bank.Note that most of the curve trends do not appear to converge at higher sample sizes.

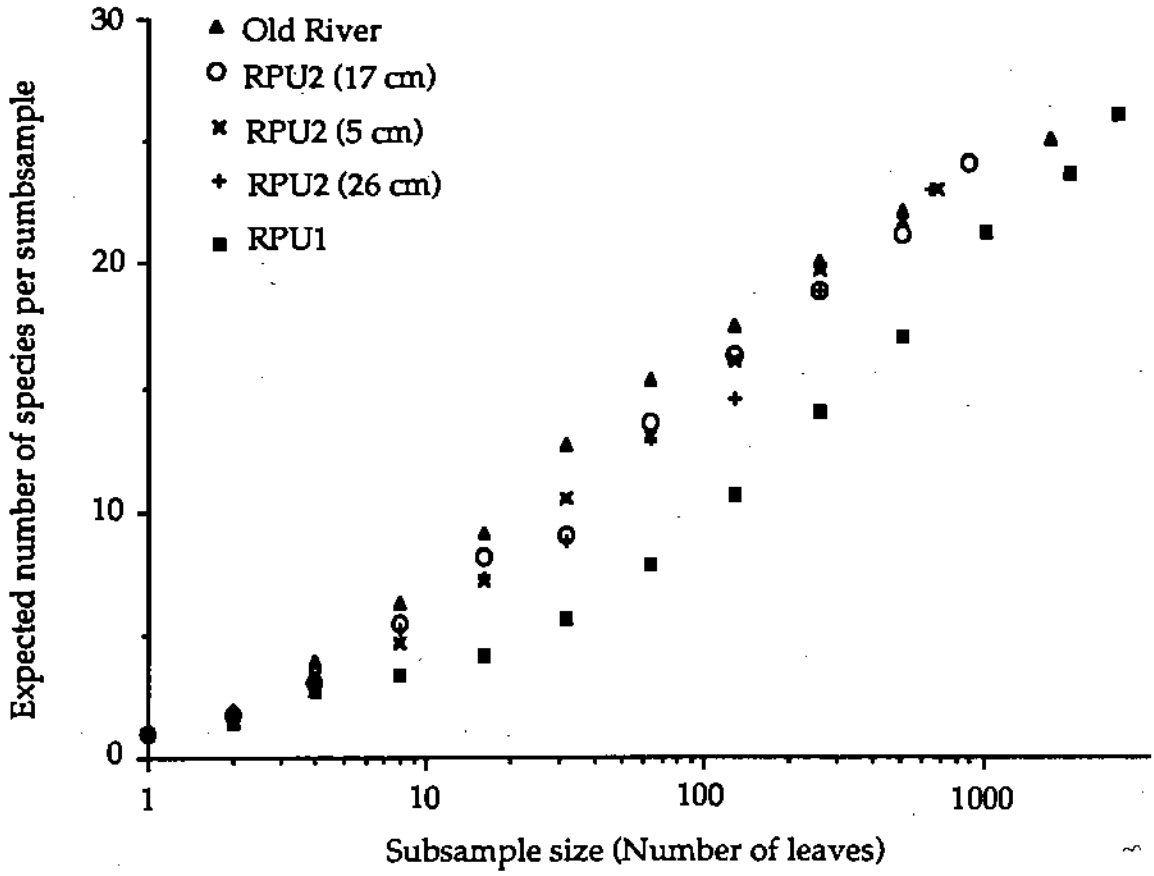


Figure 6.3 : Rarefaction curves of expected number of species *versus* number of leaves for the Regatta Point fossil sediments and the extant river bank sample Old River. Note that the RPU2 curves appear to converge with the Old River sample, and the RPU1 sample approaches the other curves at higher sample sizes.

Significant concave-up curvature occurs in the 60 cm stratum at Regency, two of the Lake Dobson samples, two of the Hastings Pool samples, the RPU1, and two of the strata at RPU2 (5 cm and 26 cm). No regression shows significant concave down curvature. The cause of this curvature is a relatively high proportion of one or two species and/or a relatively high number of rare species (e.g. at RPU1 59% of the fossils are *Allocasuarina* sp. with 11 out of 26 species each representing less than six leaves out of over 3000 leaves total; 96% of the leaves in one of the two curved Hastings samples are *Nothofagus cunninghamii*; and the other has five rare species out of seven). The magnitude of the curvature is not great in any of the samples.

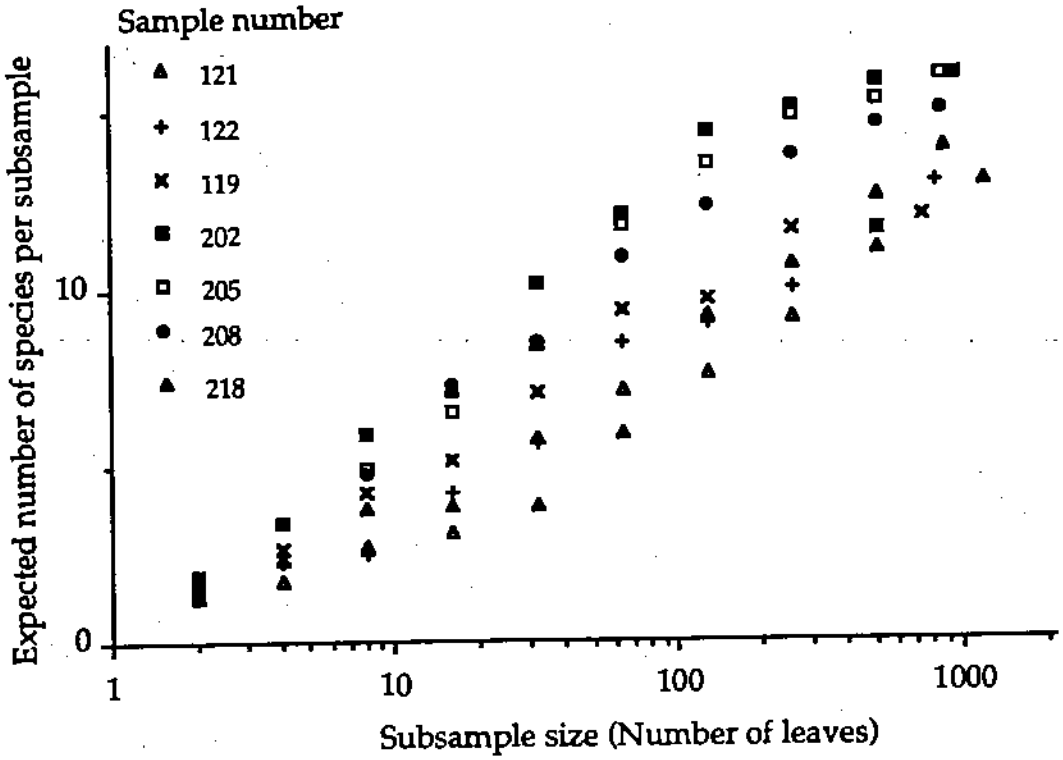


Figure 6.4 : Rarefaction curves of expected number of species *versus* number of leaves for the extant lake bottom sediment samples from Lake Dobson collected by Hill and Gibson (1985).

The trends of the expected number of species per subsample size appear to be diverging for almost all sites which have significant differences at the 128 leaf sample size. RPU1 appears to converge towards the RPU2 and Old River lines for larger sample sizes (Figure 6.3). Any other convergence appears unlikely within reasonable sample sizes. Comparisons at a constant subsample size of 128 leaves therefore give a reasonable estimate of the overall diversity of the samples. Since curvature is concave up in all cases with significant curvature, the 128 leaf subsample will underestimate the relative position of the sample at higher subsample sizes, but this does not affect qualitative differences between samples until the lines converge.

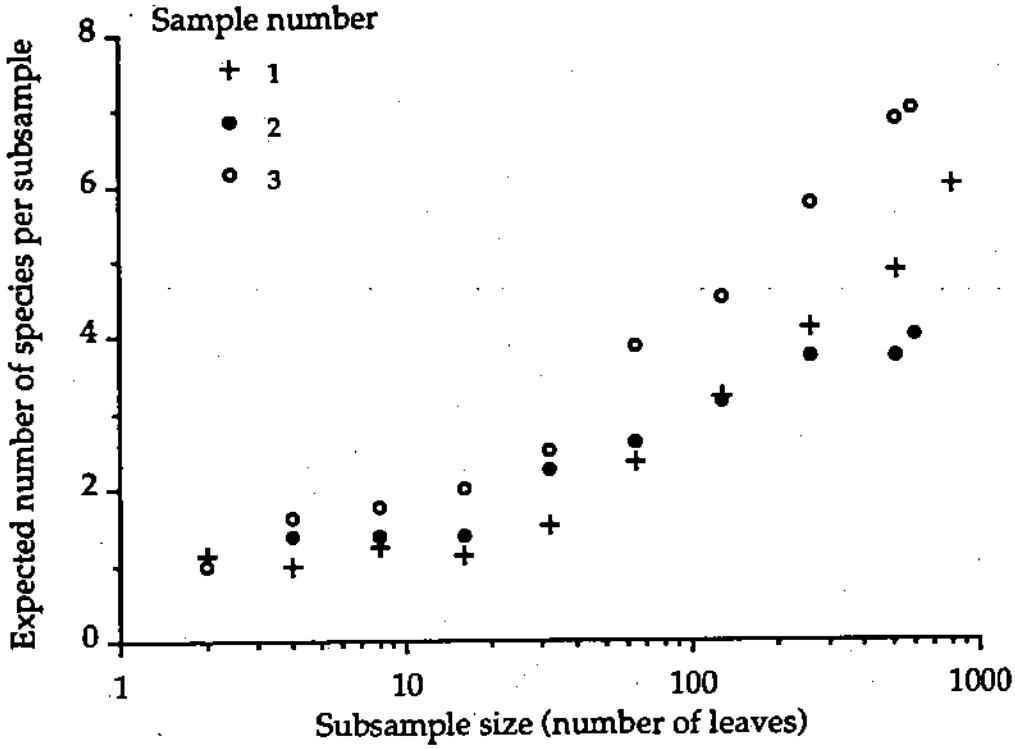


Figure 6.5 : Rarefaction curves of expected number of species *versus* number of leaves for the extant lake bottom sediment samples from Hasting's Pool.

6.4 : Discussion

6.4.1 : Factors affecting Fossil Diversity Measures

The diversity of sediments tends to be lower than that of the surrounding vegetation for the following reasons. Many plant taxa are unlikely to appear in sediments e.g. herbs, low shrubs and mesophyllous plants, but also many other taxa for less obvious reasons (e.g. *Eucalyptus* - see chapter 4). These poorly represented groups make up large proportions of the local vegetation in many vegetation types. Thus, only 26 species out of the (approximately) 150 vascular plant species in the diverse flora surrounding the lake are represented in more than 28,000 leaves sampled from Lake Dobson by Hill and Macphail (1985). Only four species of seed plant and one fern were found in the Hastings Pool sediments (see chapter 4), but eight seed plant species and at least five ferns were common nearby. 21 and 14 species, respectively were found in the Old River and Melaleuca Creek litter samples (see Chapter 4) but the local

vegetation contained over 100 species in each case. Thus only a subset of a vegetation type is likely to be represented as macrofossils in sediments. Non-woody plants, in particular, are rarely preserved as macrofossils. This assessment of diversity is, therefore, based on woody plants.

The use of composite samples of different times, or localities is likely to introduce a bias to these results. Vegetation changes over time, with the result that the smaller samples making up a composite sample are not derived from the same pool. This is an effect of non random distribution of species within the samples. Clumped distributions, such as these just mentioned, will cause overestimation of the diversity, and overdispersed distributions will cause underestimation (Simberloff 1979). Overdispersed species distributions seem unlikely to occur in samples derived from leaf litter.

Comparisons must made between the fossil sites and the extant sites with caution. Significantly, almost all leaves in the extant samples are correctly assigned to species, since the observer was familiar with the species present in local vegetation, whereas many taxa in the fossil samples go unrecognized, and may be hidden in groups such as 'microphylls'. These hidden taxa do not contribute to the diversity measure, so the sample diversity estimates for fossil sites underestimate the diversity of the source vegetation relative to the diversity estimates of extant samples. The older the fossil site, the more the measure of diversity is likely to underestimate the diversity of local vegetation, because of the higher proportion of unidentified taxa. An opposite effect is possible where more than one taxon is identified where only one was really present in the vegetation. This is unlikely to be significant in this analysis since only clearly distinct taxa were used, and almost all were assigned to modern groups.

The quality of preservation of the fossils will also affect the relationship between source vegetation and sample diversity. Poor preservation conditions will favour the most robust taxa (e.g. many Proteaceae, *Nothofagus* spp., Casuarinaceae and conifers). If any of these are common in the source vegetation they will dominate the samples at the expense of other taxa, and diversity measures of the samples will usually

underestimate the diversity of source vegetation. Certainly one or more of these taxa dominate each of the fossil samples. The two extant river litter sample sites, Old River and Melaleuca Creek, are better preserved than the extant lake sediment samples, and therefore probably relatively overestimate the source vegetation diversity (e.g. the source vegetation of the Lake Dobson samples is very diverse subalpine woodland, which is more species rich than the source vegetation of the Old River sample and of the Melaleuca Creek sample but the sample diversities of the Lake Dobson samples are less than the Old River and scarcely higher than the Melaleuca Creek sample). The extant lake sediments are in turn better preserved than the fossil samples, and are likely to overestimate the diversity of the source vegetation relative to the fossil samples. Hence, in most cases the fossil samples will underestimate the diversity of source vegetation compared with extant samples, especially the river samples.

One significant effect which may distort the diversity estimates is the leaf catchment size of the sediments, i.e. the area from which the leaves in the sediments are derived. If the catchments are heterogeneous, which almost all vegetation is, larger catchments are likely to produce higher diversity estimates than otherwise equivalent catchments. This is likely to account for a significant amount of the difference in diversity between the extant samples.

A distant source of robust taxa may introduce significant proportions of these taxa, which may increase the diversity. The extant Old River sample has higher diversity than the extant Melaleuca Creek sample. The local vegetations of these two sites are similar, but Old River has a rainforest pocket about two kilometres upstream which contributes five taxa to the litter samples, increases the diversity measure and probably explains much of the large difference between the Old River and Melaleuca Creek sites.

6.4.2 : Overall Diversity

The diversity of the vegetation contributing to the RPU2 sediments is likely to have been significantly higher than the diversity of the vegetation contributing to the Regency sediments. The sediment diversities differ greatly (Figure 6.1) even though the sites are comparable since both are

very well preserved, and their floristic compositions suggest sources from broadly similar vegetation types, with both sclerophyll and rainforest contributions. The catchment sizes of the two sites may have differed, but RPU2 has all the species present in Regency except *Phyllocladus* (of which there is pollen), and *Eucalyptus* (which is a poor candidate for fossilization). If local riparian vegetation at the time of deposition of the Regency sediments was as diverse as that of the local vegetation at the time and place of deposition of the RPU2 sediments and the differences were the result of catchment size, then one would expect to find species in the Regency sediments that are not present in the RPU2 samples.

The diversity measures in the Melaleuca Inlet, RPU1 and Little Rapid River fossil samples are likely to be relative overestimates of the diversities of their component samples, because they are composite samples. This also makes comparisons between the diversity of the contributing vegetation for the other fossil sites more difficult to make. However, source vegetation of the Little Rapid River site is likely to have been diverse. The presence of a large group of unidentified and possibly cryptic taxa, however, is likely to cause large underestimation of the diversity, since these taxa are mostly uncommon and not included in the analysis. This effect occurs with all the fossil sites, but is most severe at Little Rapid River, and least significant at Regency and Melaleuca Inlet where the taxa are almost all modern and readily recognisable.

The estimate for the Melaleuca Inlet fossil site may be a relative overestimate because the similarity in floristic composition to the Old River litter sample suggests a distant source of easily preserved taxa. The Old River sample represents vegetation which is amongst the most diverse of lowland riparian vegetation in western Tasmania. The relatively high diversity of the Melaleuca Inlet sample is expected because it is floristically similar to the Old River site.

The Melaleuca Inlet and RPU1 sites were probably moderately diverse and possibly more diverse than Regency and less diverse than RPU2, since the samples were overestimates due to the bulking effect. It is likely that the diversity of the source vegetation of the Little Rapid River sample was high by modern Tasmanian standards. The source vegetation

of the RPU2 samples was also probably at least as diverse as the most diverse modern day lowland riverine vegetation in Tasmania, since the diversity measure is as high as that of the Old River sample which probably gives a relative overestimate of the diversity of the source vegetation. The RPU2 sample diversities are also higher than those of the Lake Dobson samples, which are derived from a robust and diverse source vegetation. The RPU1 sample probably came from source vegetation which was less diverse than the RPU2 sample, but this is confused due to the poorer preservation of the RPU1 samples and the effects of using a bulk sample. The Regency samples probably came from vegetation which was considerably less diverse than the RPU2 vegetation and possibly the RPU1 vegetation. It is difficult to assess the relative diversity of the source vegetation of the Melaleuca Inlet samples, but it is likely to have been significantly lower than that of the RPU2 samples since there are several indications of relative overestimation.

The diversity of modern rainforest (e.g. Hastings Pool) is lower than those of the source vegetations of all the fossil sites, although Hastings Pool is particularly low since it has a very small catchment. Each of the extant and fossil sites except Hastings Pool probably represents some form of gallery forest, with a mixed composition. Hence, comparison of the sites can give some indication of the trends in diversity of the gallery rainforest with time.

Hence, in summary the diversities of the source vegetation of the samples are likely to follow this order :

Little Rapid River (fossil : Oligocene) > RPU2 (fossil : Early Quaternary) > RPU1 (fossil : Early Quaternary) ≥ Old river (extant : diverse) ≥ Melaleuca Inlet (fossil : Late Quaternary) ≥ Lake Dobson (extant : diverse) ≥ Melaleuca Creek (extant : diverse) > Regency (fossil : Early - Middle Quaternary) > Hastings Pool (extant : species poor).

6.4.2 : Rainforest Diversity

Tasmania's extant rainforest has low species diversity. Jarman *et al.* (1984) list only 73 rainforest seed plant species in Tasmania, at least 21 of which are exclusively high altitude species, and many of which also occur

in non-rainforest habitats. Seven of the seed plant species occur as canopy trees in rainforests of lowlands or moderate altitudes. The pteridophyte flora is rich, with about 46 species (Jarman *et al.* 1984). The bryophyte flora of Tasmanian rainforest is rich by world standards with several hundred species (Scott *et al.* 1976, Scott 1985). Only some of these species will occur in any one locality. The most diverse lowland rainforest in Tasmania occurs in western and south-western Tasmania.

Table 6.5 shows that of the 49 woody seed plant species recorded in Jarman *et al.* (1984) 17 species, or their close relatives, occur in Regatta Point sediments, 16 in RPU1 and 10 in RPU2. Sediments derived from modern day forest are unlikely to contain more rainforest species than this for the reasons explained below. The presence of more extant rainforest taxa in the RPU1 sediments than in RPU2 sediments may be because the RPU1 sample is derived from several blocks of sediments probably of different age (or possibly transported from different areas) (see above). The sizes of the samples are similar. Not all the taxa co-occur in the same strata, but all the common ones do (e.g. *Nothofagus cunninghamii*, *Eucryphia* sp., *Lagarostrobos franklinii*, *Athrotaxis* cf. *laxifolia*, *Trochocarpa* sp. and *Phyllocladus asplenifolius* can be seen together in single strata).

Table 6.6 lists the woody species which occur in modern Tasmanian rainforest but which do not occur as fossils in either the RPU1 or RPU2 sediments. All but seven of these can be discounted as being unlikely to appear in modern day lowland leaf deposits, either because they are uncommon or rare in lowland western Tasmania, because they have thin, soft leaves, or because they are unlikely to be identified. Only one of these seven species is a common tree species of rainforest (*Anodopetalum biglandulosum*). The taphonomic work at Hastings Pool and Old River suggests that leaves of *A. biglandulosum* are unlikely to be found in sediments, and pollen consistent with this species (but also with *Eucryphia*) is present in the sediments, although only in trace amounts in RPU2. The other taxa are four shrubs and one woody climber, which are not likely to be strongly represented in sediments (see chapter 4), and one small tree (*Pittosporum bicolor*). Pollen possibly attributable to two of these taxa (*Pimelea*/*Drapetes* pollen for *Pimelea drupacea*, and *Monotoca* pollen for

Table 6.5 : Woody rainforest species in Tasmania according to Jarman *et al.* (1984) which occur in the Regatta Point sediments, or a very close relative does. ~~+ in the columns 'RPU1' or 'RPU2' indicate the presence of this taxon at that site.~~ *Podocarpus lawrencii* is not included in Jarman *et al.* (1984) as a rainforest species, but is likely to have been one at the time of deposition of the RPU1 sediments.

Fossil species	Extant species	Comments
Species at both RPU1 and RPU2		
Agastachys odorata	*A. odorata*	Shrub
Athrotaxis cf. *laxifolia*	*A. selaginoides*	Common tree
aff. *Cyathodes juniperina*	*C. juniperina*	Shrub
Eucryphia species	*E. lucida*	Common tree
Lagarostrobos franklinii	*L. franklinii*	Common tree
Nothofagus cunninhamii	*N. cunninhamii*	Common tree
aff. *Richea milliganii/R. acerosa*	*R. milliganii*	Uncommon shrub
Telopea cf. *mongaensis*	*T. truncata*	Tree/shrub
Trochocarpa sp.	*T. gunnii*	Common shrub
Species only at RPU1		
Acradenia species	*A. franklinae*	Rare
? *Anopterus* species	*A. glandulosus*	Common shrub
Atherosperma moschatum	*A. moschatum*	Common tree
Cenarrhenes nitida	*C.nitida*	
Phyllocladus aspleniifolius	*P.aspleniifolius*	Common tree
Podocarpus species	*P. lawrencii*	Alpine / sub-alpine shrub
Tasmannia ? *lanceolata*	*T. lanceolata*	
Species only at RPU2		
Orites sp. nov.	*O. diversifolia*	

Table 6.6: Woody rainforest species in Tasmania according to Jarman *et al.* (1984) which do not occur in the Regatta Point sediments and comments on why many of them are unlikely to be found.

Species	Comments
Anodopetalum biglandulosum	
Archeria eriocarpa	
A. hirtella	Unlikely to be distinguished from *A. eriocarpa*
A. serpyllifolia	High altitude
Aristotelia peduncularis	Soft mesophyllous leaves
Athrotaxis cupressoides	High altitude
A. laxifolia	High altitude
Clematis aristata	Soft mesophyllous leaves
Coprosma nitida	High altitude
Coprosma quadrifida	Thin soft leaves
Cyathodes parvifolia	High altitude
Diselma archeri	High altitude
Dracophyllum milliganii	Uncommon at low altitude
Epacris mucronulata	Uncommon
Eucryphia milliganii	High altitude
Gaultheria hispida	
Leptospermum riparium	Uncommon
Monotoca glauca	
M. submutica	Uncommon in rainforest
Notelaea ligustrina	Uncommon in western Tasmania
Nothofagus gunnii	High altitude
Olearia persoonioides	High altitude
Orites milliganii	High altitude
Pimelea cinerea	Uncommon
P. drupacea	
Pittosporum bicolor	
Prionotes cerinthoides	
Pseudopanax gunii	Uncommon
Richea pandanifolius	Leaves are too large (mostly 1-1.5 m long)
R. scoparia	High altitude
Tetracarpaea tasmanica	High altitude
Trochocarpa cunninghamii	Unlikley to be distinguished from *T. gunnii*
T.disticha	Rare

M. glauca) occurs in both the RPU1 and RPU2 sediments (M. K. Macphail pers. comm.; Hill and Macphail 1985). The remaining three species are two epacrids and one member of the Ericaceae, which in general have poor cuticle, and two of these (*Prionotes cerinthoides* and *Gaultheria hispida*) are amongst the most mesophyllous members of the Ericales found in Tasmania. These 'missing taxa' are, therefore, considered to be unlikely to be represented as macrofossils.

Of the six taxa which are present in the RPU1 sediments, but not in the RPU2 sediments, the modern equivalent of one (*Acradenia* sp.) is rare and two more (*Anopterus* sp. and *Atherosperma moschatum*) are clearly poor candidates for preservation (see the results for Hastings Pool and note that these taxa are only known from single impressions in RPU1). Pollen of *Anopterus* and pollen which is probably *Tasmannia* occur in the sediments. *Phyllocladus asplenifolius* is a notable absence. However, small amounts of *Phyllocladus* pollen occur in the sediments (M. K. Macphail pers. comm.). Thus, *Cenarrhenes nitida* is the only notable absence from RPU2. *Orites diversifolia* is the only notable absence from RPU1.

The RPU1 and RPU2 sediments contain taxa which are now uncommon in western Tasmanian rainforest. Aff. *Richea milliganii*/*R. acerosa* occurs in both sites and *Acradenia* sp. and *Podocarpus* sp. occur in the RPU1 sediments. Thus both sites contain virtually all the lowland western Tasmanian rainforest species (or probable ecological equivalents) that are likely to occur in sediments, and some that are unlikely. Hence the RPU1 and RPU2 floras have representations of modern day woody taxa (or possible equivalents) equivalent to rainforest floras with a diversity as high as contemporary western Tasmanian rainforest. But RPU1 and RPU2 also contain macrofossils of extinct rainforest taxa with no modern day equivalent (*Rubus* sp. and *Quintinia* sp. at both sites, aff. *Dacrycarpus*/*Dacrydium* and *Laurophyllum* at RPU2 and cf. *Austromyrtus* at RPU1). *Callitris*/*Actinostrobus* species, Proteaceae genus unknown #1 and (?) Proteaceae genus unknown #2 may also have been rainforest taxa.

Microfossil evidence shows that some additional rainforest taxa were probably present at the time of deposition of the RPU2 sediments, and possibly present at the time of deposition of the RPU1 sediments (M. K.

Macphail pers. comm.). Several probable rainforest tree and shrub taxa, now extinct from Tasmania, appear as pollen in the RPU2 sediments. Some of these are unlikely to have been reworked from Tertiary sediments. Symplocaceae pollen, at least one species of the Malvaceae, and *Astelia* pollen outside of the range of extant *A. alpina* (and possibly epiphytic) occur in the RPU2 sediments. Pollen which is likely to be from more than one species of each of *Lagarostrobos*, Winteraceae and *Muehlenbeckia* occurs in the RPU2 sediments. Each of these taxa is now represented by only one species in western Tasmania. The RPU1 sediments contain pollen of *Dacrycarpus* and possibly an extinct species of *Lagarostrobos* which are likely to have been rainforest plants. Some of these have stratigraphic ranges extending back to the early Eocene or earlier and could be reworked from the Strahan Sub-basin sediments, and others could have been derived from reworking of the RPU2 sediments, if these sediments are indeed older.

It is therefore highly likely that the Regatta Point floras are derived from vegetation containing more diverse woody rainforest components than now occur in lowland Tasmania.

The Regency sediments contain a similar array of extant lowland rainforest taxa to the RPU1 and RPU2 sediments, with 11 extant rainforest species being present as macrofossils, although not all of these occur in the same strata. An additional three occur as pollen. The major tree species are all present except *Anodopetalum biglandulosum* and *Atherosperma moschatum*. As discussed above, leaves of these two species are unlikely to be preserved. This is consistent with a rainforest diversity equivalent to modern vegetation. No macrofossils of any extinct taxon, and pollen of only one extinct rainforest tree or shrub taxon, *Quintinia*, and one possible rainforest herb, *Gothanipollis* (a mistletoe of the Loranthaceae), occur in the sediments (Fitzsimons *et al.* 1990). The differences in the diversities of the fossil assemblages indicate that the diversity of the woody rainforest component of the source vegetation of the Regency sediments was lower than that of the Regatta Point sediments. The sedimentary environment at Regatta Point is poorly understood, so a larger catchment may have contributed macro- and microfossils to this site than at Regency. The

differences are so large, and Regency differs so little from modern vegetation that the differences in diversity are unlikely to be solely the result of differences in taphonomy. In addition, about twice as many fossils were identified from the Regency samples as both RPU1&2 put together. It is, therefore, likely that the diversity of gallery forests in Tasmania at the times of deposition of the Regatta Point sediments was higher than at the time of deposition of the Regency sediments.

The composition of the rainforest components of the Melaleuca Inlet sediments is similar to that of the modern rainforest in the region except for the absence of taxa unlikely to fossilize, so there is no reason to assume any difference in diversity from modern forest of the region.

6.4.3 : Sclerophyll Diversity

There are indications that there has been a decline in diversity of some sclerophyll groups in Tasmania. *Banksia marginata* is the only species of *Banksia* now widespread in Tasmania, where it has a huge ecological range, but *B. serrata* occurs in a very restricted locality in north-west Tasmania (Taylor and Hopper 1988). In Tasmania *B. marginata* occurs in cool open woodland on reasonably well drained sites, oligotrophic swamp country in high and low rainfall areas, in wind and salt pruned coastal heath, on less exposed coasts, in coastal woodland and sandy heaths and in association with cool temperate rainforest regrowth. It also occurs widely in south-eastern mainland Australia, but it has a more restricted range of habitats : it is largely restricted to cool open woodland on reasonably well drained sites, although occasional plants occur in other habitats. It also occurs in semi-arid areas, but this habitat does not occur in Tasmania. Other species of *Banksia* occur on the mainland in habitats types occupied in Tasmania by *B. marginata*. *B. robur* occurs in swamps and *B. ericifolia*, *B. paludosa* and *B. oblongifolia* in other poorly drained areas, *B. canei* and *B. saxicola* occur in subalpine woodlands, *B. spinulosa*, *B. saxicola* and *B. conferta* occur in cool wet woodland, *B. spinulosa* var. *neo-anglica* and *B. integrifolia var. compar* in vegetation mosaics associated with cool temperate rainforest regrowth, trees of *B. integrifolia* var. *integrifolia* often occur on sandy seashores, *B. aemula* and *B. serrata* occur in coastal woodland and *B. paludosa* and *B. spinulosa* and other species

occur in headland heath (Taylor and Hopper 1988; George 1984; personal observations). Often more than one species of *Banksia* occurs at the same site.

At least two species of *Banksia* have become extinct in Tasmania during the Pleistocene. *Banksia kingii* became extinct in Tasmania after the deposition of the Melaleuca Inlet sediments, and *B. strahanensis* became extinct after the deposition of the Regatta Point sediments. Additionally, a species similar to *B. kingii* was present at the time of deposition of the Regatta Point sediments. It is also likely that *B. marginata* was extant early in the Pleistocene, since it seems to be morphologically consistent over its whole range, is relatively poorly dispersed, and now has a very wide geographical distribution (from far northern New South Wales, to the Eyre Peninsula in South Australia, to southern Tasmania). It also occurs on Tasmanian offshore islands which contain woodland habitats, even those which were not connected by land to mainland Tasmania during the low sea level periods of the glacials. It is unlikely that a relatively poorly dispersed species could have reached all these areas if it were a recent arrival.

This apparent anomaly in the distribution of *Banksia* species has several possible explanations :

(1) More species of *Banksia* occurred in Tasmania early in the Pleistocene than now occur, most of these became extinct and *Banksia* has not speciated or recolonised from other areas to fill the niches vacated by the extinctions, i.e. the niches were lost, probably during glacials, but now exist once again during the current interglacial. *Banksia marginata* has therefore extended its ecological role to occupy these vacant niches. This hypothesis is supported by the morphology of *B. marginata*, which appears to be more variable in Tasmania than on mainland Australia, and this variation corresponds approximately to differences in habitat. This may be diversification of *B. marginata*, and a stage in speciation.

(2) More species of *Banksia* occurred in Tasmania early in the Pleistocene than now occur, most of these became extinct due the loss of ecologically essential species which no longer occur in Tasmania. Several of the species mentioned from south-east Australia, however, (*B. serrata*, *B.*

integrifolia var. *integrifolia*, *B. spinulosa*, *B. ericifolia* and *B. robur*) now grow vigorously. The other species mentioned are little cultivated in Tasmania (Wrigley and Fagg, 1989). It is unlikely that pollinators are missing since these species produce seed in cultivation in Tasmania. In addition, obligate plant/vertebrate mutualisms are very rare (Reid 1991). Interactions with invertebrates are a possibility.

(3) There are more niches available for *Banksia* species on mainland Australia, directly or indirectly due to climate or edaphic features. However, five species of *Banksia* grow at Wilson's Promontory which is climatically and edaphically similar to parts of Tasmania.

There are several other examples of species with very wide ecological ranges in Tasmania and which have congeners occupying similar niches on the mainland (e.g. *Grevillea australis, Acacia melanoxylon* and *Leptospermum scoparium*). It seems likely that these species have expanded their ranges to take in niches vacated by earlier extinctions. Like *B. marginata, G. australis* is morphologically more diverse in Tasmania than on the mainland, and has been divided into several subspecies, though it is likely that these subspecies are not disjunct morphologically (R. O. Makinson pers. comm.). There are numerous species of *Grevillea* in south-eastern Australia, but only one in Tasmania (Wrigley and Fagg 1989). It is not clear whether the other species mentioned are more morphologically diverse in Tasmania, or on the mainland.

6.4.5 : Extinct Tasmanian Taxa

Pollen of a relatively broad range of herbaceous taxa* is present in all the sediments. Some of these taxa are extinct, but they do not help greatly in assessing the diversity of herbaceous taxa. The changes in diversity of woody plants through the Pleistocene seem to involve a decrease in diversity. When a large number of woody taxa become extinct it is likely that a number of herbaceous taxa will also become extinct unless the causes of the multiple extinctions are specific to woody taxa. There is no indication that this was the case in the extinctions described here. Hence, non-woody plants are also likely to have become extinct during the Early-Middle Pleistocene. The amount of habitat of some classes of non-woody

* (See Hill and Macphail (1985); Fitzsimons et al. (1990); Jordan et al (1991))

plants probably increased, especially in the Late Pleistocene. The amount of sedgeland-heath probably increased markedly during the Late Pleistocene (Macphail & Colhoun 1985; Jordan *et al.* 1991) probably in response to increased fire frequencies. The increase in habitat may have been associated with an increase in number of non-woody plants and woody plants associated with high fire frequencies living in Tasmania, but it is not possible to estimate the effects of this on more local diversity.

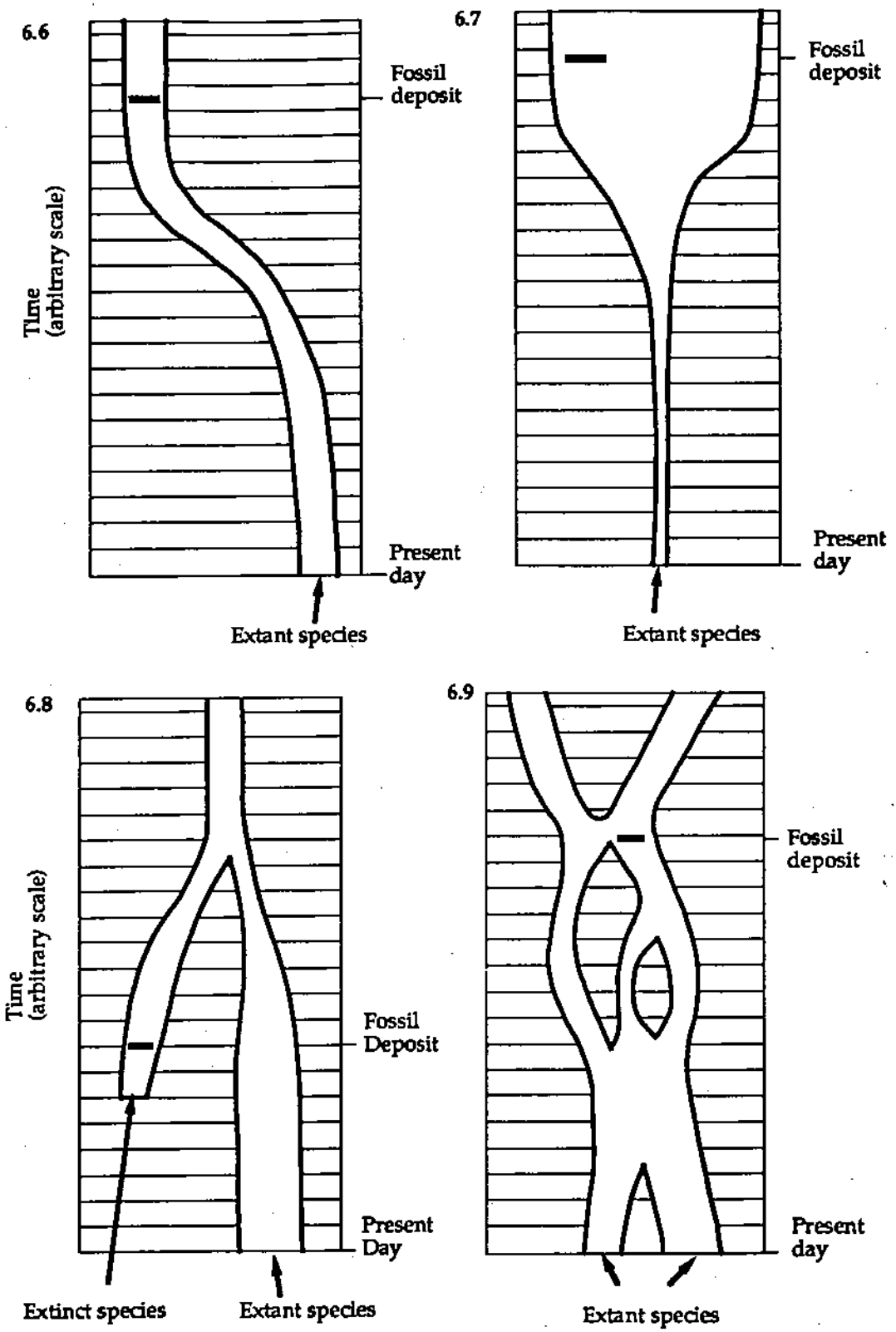
6.4.5.1 : Taxa With Close Extant Relatives Still In Tasmania

Some of the extinct species found in RPU1 and RPU2 have close relatives living in Tasmania. In each case, fossils of the close extant relatives do not appear in the sediments. The taxa are *Anopterus* sp., *Banksia* cf. *kingii*, *Callitris*/*Actinostrobus* sp., *Orites* sp. and *Telopea* sp. *Allocasuarina* sp. and *Athrotaxis* sp. are also likely to be extinct species, and appear to be closely related to modern species. Other taxa which appear to differ from their modern Tasmanian counterparts, but for which the evidence of extinction is less clear cut, are *Podocarpus* sp., *Eucryphia* sp. and even possibly *Nothofagus cunninghamii*.

For all of these taxa, absence from the present flora may be taken as evidence of one of three possibilities :

(1) Both the extinct form and the ancestors of the close extant relative(s) were extant, and genetically separate at the time of deposition, and one has become extinct since that time (Figure 6.8). Such extinctions are likely to have produced some relaxation of the ecological constraints on the surviving species, which may have allowed a morphological radiation of these species (Figure 6.13), as has been suggested above for *Banksia*.

(2) The extinct taxon is ancestral to the extant taxon. This may have involved simple evolution of one species (Figure 6.6), or it may have involved a more complex path. Several authors have suggested that within groups of closely related species sufficient gene flow occurs such that species are constructed out of parts of other species. The coenospecies concept of Stebbins (1950) proposes that groups of freely interbreeding species function as single gene pools with peaks of abundance of those genotypes which produce phenotypes favoured by current conditions.



Figures 6.6 to 6.9 : Stylized representations of some possible changes in morphological range of species with time. The horizontal axis is an idealized measure of the morphological range of the taxon. The bars indicate the morphological range of fossil forms. The vertical axis is an arbitrary time scale. Figures 6.6 - 6.9 represent ways in which an extinct fossil form can have an extant close relative in the same region. 6.6 : The fossil form evolves into another form. 6.7 : A diverse form in the past is reduced in morphological range. 6.8 : A species becomes extinct, but a close relative persists. 6.9 : A group of morphologically distinct forms interbreed readily, and different forms are favoured by different conditions.

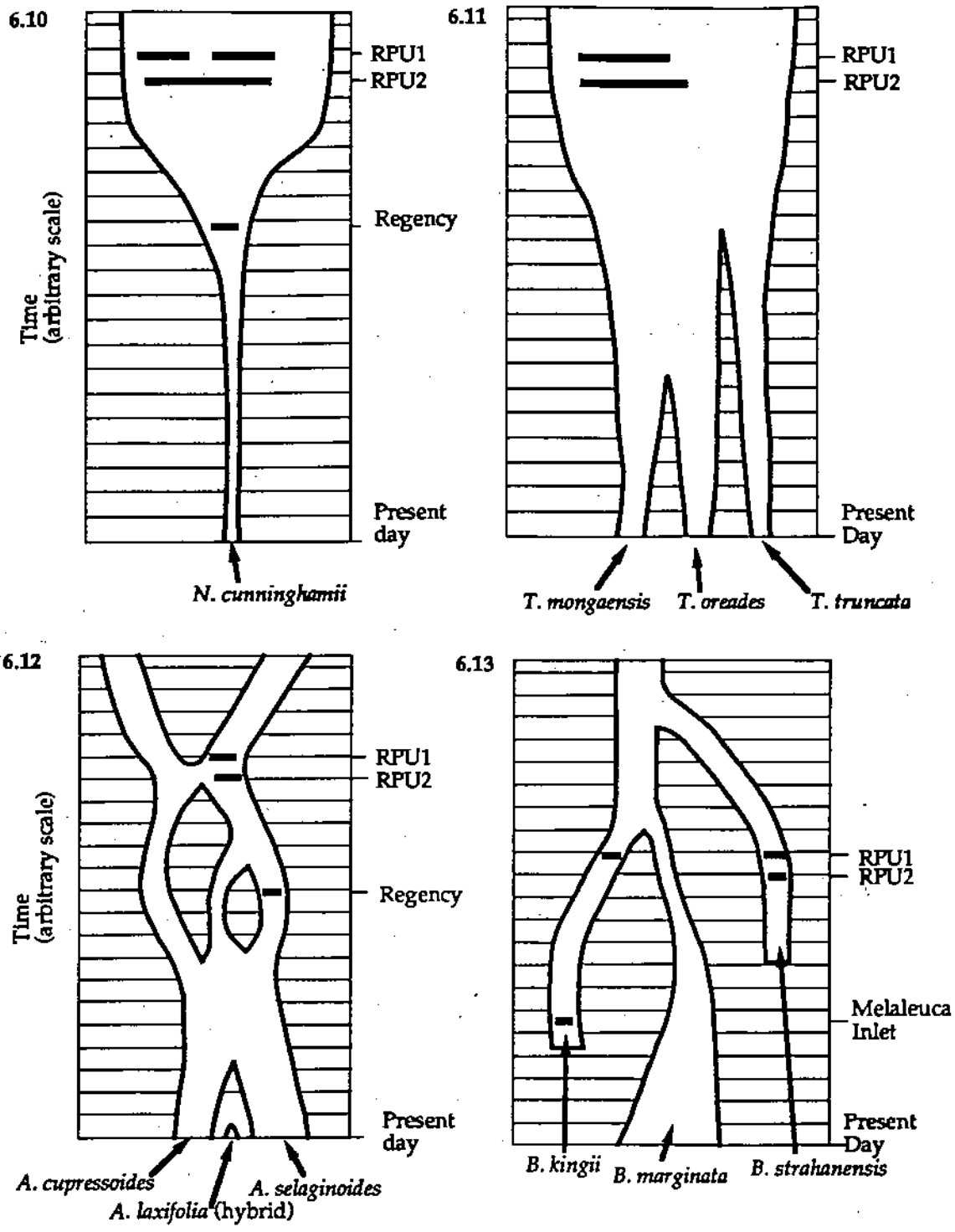


Figure 6.10 - 6.13 : Some hypotheses relating to some taxa described in this study. RPU1 is not necessarily older than RPU2. The axes are explained in the caption to Figures 6.6-6.9. 6.10 : Fossil *Nothofagus cunninghamii* found at Regatta Point appears to be more variable than any extant population. This variation is at times bimodal. By Regency, this variation had been reduced to modern levels. Variation in the species may have reduced within poulations. 6.11 : Fossil *Telopea* in the Regatta Point sediments appears to be more variable than the extant species. A variable species may have subsequently split into races which are now recognised as species. 6.12 : *Athrotaxis* macrofossils in RPU1 and RPU2 appear to be intermediate to the morphological ranges of the modern species. The extant species appear to hybridise relatively freely, so some reticulate evolution may have occurred. 6.13 : Fossils of now extinct species of *Banksia* appear to be from separate lineages from the extant Tasmanian *B. marginata*. In Tasmania *B. marginata* is very diverse ecologically and morphologically. It may have radiated after the extinction of the other taxa.

These favoured phenotypes are the recognised species. Since these taxa hybridize freely, with fully viable progeny, under altered conditions other morphologies would be selected within the constraints allowed by the gene pool of the group. The processes of geographic disjunction and reunification caused by environmental change would also amplify this process. If there is little loss of the gene pool through extinction of types then this process can continue repeatedly. Such a scenario is illustrated in Figure 6.9. Ogden (1989) proposed that this process may have acted in several groups in New Zealand to construct and reconstruct morphologies during the cyclic climatic variations of the Pleistocene. Several groups of major ecological significance in New Zealand are candidates for this process. For example free introgressive hybridization appears to occur within *Nothofagus* subgenus *Fuscaspora* (Wardle *et al.* 1988), and within *Podocarpus* (Wardle 1972) in New Zealand. Such processes would explain the presence of morphologies outside the range of the modern species in the Regatta Point sediments particularly in the case of *Athrotaxis* (Figure 6.12), where there is continuous variation between the modern species (*A. selaginoides*, *A. cupressoides* and the putative hybrid *A. laxifolia*), and the fossil taxon scarcely differs from the hybrid form. The strongly bimodal distribution of leaf lengths in *N. cunninghamii* leaves from RPU1 could also be explained in these terms. The process of simple substitution of morphological types is unlikely to have occurred in poorly dispersed taxa for which the closely related extant species have widespread distributions (such as *Allocasuarina verticillata*).

(3) Species may have been much more variable in the past than at present. Some of these 'extinct' fossil species may in fact have been parts of very variable species which are now considerably reduced in morphological range. The morphological variation of several taxa in the fossil sediments appears to be higher than morphological variation in their extant relatives, e.g. *N. cunninghamii* (See chapter 5) (Figure 6.10). *Telopea* sp. shows greater morphological variation in leaf shape and particularly in cuticle morphology than extant species of *Telopea* (see chapter 3) (Figure 6.11). These taxa indicate that the processes of extinction through the Pleistocene may not only have involved the extinction of

species, but also the significant reduction of gene pools within species.

There is no compelling evidence available at present to choose between these three options for most of the species described as extinct in this thesis. The presence, however, of *Banksia kingii* in the Melaleuca Inlet sediments cannot be explained in terms of direct evolution of one form into another because of the widespread distribution of its close relatives, but can be explained by the processes of extinction, reticulate evolution or reduction of diversity. Similarly, the strong probable ecological differentiation, and morphological distinctiveness of *Callitris/Actinostrobus* sp. (from Regatta Point) from the species extant in Tasmania, together with widespread modern distribution of *C. rhomboidea* suggests that the fossil species is unlikely to be ancestral to the modern species. The greater morphological range of fossil *N. cunninghamii* and of *Telopea* sp. from Regatta Point compared to extant *N. cunninghamii* and *T. truncata* implies that there has been a reduction in diversity either by extinction of species not clearly distinguishable as macrofossils, or by the reduction in the morphological range within these species.

6.4.5.2 : Taxa Without Close Extant Relatives Still in Tasmania

Other taxa in the sediments have no close relatives extant in Tasmania, and therefore their presence is unambiguous evidence of extinctions of lineages from Tasmania. These are *Banksia strahanensis*, *Oxylobium* sp., *Rubus* sp., *Quintinia* sp., aff. *Austromyrtus*, *Acacia* sp., aff. *Dacrycarpus/Dacrydium*, *Laurophyllum* species and the two extinct probable proteaceous species of unknown affinity. Of these species, *Rubus* sp., *Quintinia* sp., aff. *Austromyrtus*, aff. *Dacrycarpus/Dacrydium* and *Laurophyllum* species have clear similarities and affinities to taxa which now occur in areas less prone to summer drought than Tasmania (New Zealand and/or the wet forests of the Great Dividing Range of eastern mainland Australia) . Areas may have existed during the glaciations in New Zealand and the Great Dividing Range which were less droughted than in western Tasmania. Drought periods may have contributed to the demise of these taxa. However, one of these taxa, *Quintinia*, existed in Tasmania until the Last Interglacial (Fitzsimons *et al.* 1990), but its distinctive pollen type is

unknown from the well recorded Margaret (Last) Glaciation or the Holocene. It survived through several glaciations, but probably became extinct during the Last Glaciation.

All of these extinct wet forest taxa except *Laurophyllum* have close extant relatives living in areas of New Zealand which are as cool as, or cooler than, Tasmania. Otherwise, the cold of the glacials may have contributed, but this does not explain the persistence of their relatives in New Zealand. Today the Lauraceae are restricted to warmer climates than Tasmania, so temperature may have played a role in this case. The role of changes in CO_2 (see chapter 2) in extinctions during the Late Cainozoic is an area entirely open to conjecture.

For reasons discussed in Chapter 2 the land bridges present at various times in the Pleistocene between Tasmania and mainland Australia were probably unsuitable habitats for drought intolerant species. These landbridges, therefore, would not have provided corridors for the dispersal of the extinct wet forest species since these species probably had limited capacity for long distance dispersal across water.

The extinction of *Banksia strahanensis* and *Oxylobium* cf. *ilicifolium*, which occur in the Regatta Point sediments, are less easily explained as direct climatic effects. They both have close relatives (*B. spinulosa* var. *spinulosa* and *B. spinulosa* var. *cunninghamii* and *O.* '*staurophyllum*') which are morphologically very similar, and presumably with some ecological similarity, which live in areas drier and as cool as, or cooler than, lowland western Tasmania (e.g. at high altitude in the Blue Mountains). Both extinct taxa have morphological features which are typical of plants from cold, dry or oligotrophic conditions. *Banksia strahanensis* has narrow, sclerophyllous, revolute margined leaves. *Oxylobium* cf. *ilicifolium* has narrow lobed, pungent, sclerophyllous leaves.

Similarly, the Late Pleistocene or Holocene extinction of *Banksia kingii* is difficult to explain. Two possible causes of the extinction of *B. kingii* are the climatic disturbances of the last glaciation and/or increased fire frequency due to human activity. There are difficulties with both of these explanations. Extant *Banksia* species are generally highly fire adapted. The *Banksia kingii* infructescences show some unopened follicles and seeds

persistent in other follicles (Fig. 24), which suggests that the seeds were retained for some time on the plant. The retention of seeds is a common fire adaptation in *Banksia* (George 1984). The follicles are also very thick, which would allow for some protection of the seed from fire. *Banksia kingii*, therefore, was probably adapted to seed release following fire. *Banksia kingii* persisted into the Late Pleistocene and must, therefore, have tolerated the rapid changes of climate and landform of the Middle Pleistocene only to die out later. The close relatives of *Banksia kingii* are *B. saxicola* and *B. canei* which occur in cool to cold, moist areas of Victoria and New South Wales (Taylor and Hopper 1988), mostly on siliceous soils. The leaves of these species approach the robustness of *Banksia kingii* only on plants growing in exposed, moderately wet, high altitude areas (e.g. *B. saxicola* on the summit of Mt. William (1200 m a.s.l.) in the Grampian Range of Victoria and *B. canei* from the top of the Kybean Range of south-eastern New South Wales (1250 m a.s.l.)). Both these sites have skeletal, siliceous soils so *Banksia kingii* was probably adapted to harsh, and cold but not particularly dry conditions.

An alternative hypothesis for the cause of extinction of the more sclerophyllous taxa may be that they were intolerant of interglacial conditions. Tasmania is the southern end of a continent, separated intermittently by a relatively narrow water body. As such there is plenty of land to the north, but none to the south. Thus, in Tasmania, species intolerant of warmth must adapt or migrate upslope during warmer periods, or die out. Likewise, there is no source of cold adapted species to the south which can recolonise after periods of warmth. Since glacial periods tend to be much longer than full interglacial periods, some species may have become adapted to these colder and drier conditions. The interglacials would then be periods of stress for these species. Under these conditions, species adapted to cold and drier periods (such as *B. kingii*) may have become extinct or restricted during interglacials.

The Regatta Point site at the time of deposition is likely to have had a small catchment of potential macrofossils. Riparian vegetation is likely to have provided the vast majority of the fossils, and only a subset of the riparian vegetation is likely have been fossilized (see Chapter 4). Thus

these sediments must contain fossils of only a very small proportion of the plant species extant in western Tasmania at the time of deposition. Since the Regatta Point sediments contain several extinct taxa either the source vegetation of the fossils was an enclave of now extinct species or many other now extinct species occurred in western Tasmania at this time. As there is no reason to believe that the environment of the catchment of the Regatta Point sediments was fundamentally different to any other part of Tasmania, the latter option must be preferred.

The Pleistocene plant extinctions were almost certainly stepwise, rather than a result of a catastrophic event. It is not clear whether the Regatta Point sediments are older or younger than the Linda Glaciation, which was the most extensive of the glaciations, and presumably imposed severe climatic conditions on Tasmania. The Linda Glaciation must have occurred either between the times of deposition of the Linda Valley sediments and RPU (1 and/or 2), or between the times of deposition of RPU (1 and/or 2) and Regency. Decreases in the number of 'Tertiary' taxa occurred during each of these intervals. Extinctions were, therefore, almost certainly associated with climatic events other than the Linda Glaciation. Some taxa (*Gothanipollis*, *Quintinia* and *Stephanocolpites*) persisted into the Middle and Late Pleistocene.

Fire appears to have occurred throughout the Pleistocene, especially during glacials. It is possible that rainforest taxa became extinct due to expansion and retraction of sclerophyll vegetation during glacial/interstadial conditions associated with fire. There is no evidence for increasing levels of charcoal, however, until the Late Pleistocene.

Large fluctuations in palaeotemperatures occurred before the Early Pleistocene with periods of oxygen isotope ratios implying significantly lower deep sea temperatures than at present (see Figure 2.2). All the extinct taxa therefore probably survived conditions which were more severe than prevail at present. The results presented in chapters 4 and 5 suggest that the climate at the time of deposition of the RPU1 sediments was cooler than at present, and little or no warmer at the time of deposition of the RPU2 sediments than at present. There is, therefore, probably no feature in modern day climates which prohibits the occurrence of diverse rainforest in

Tasmania.

This extinction of plant taxa is also likely to have been associated with a loss of faunal diversity. Lower animal diversity may have exacerbated the difficulties in re-establishing high plant diversity and *vice versa*. An example is the pollen record of the Loranthaceae from Late Tertiary and the Early and Middle Pleistocene in Tasmania, and its subsequent disappearance (Fitzsimons *et al.* 1990.; M. K. Macphail pers. comm.). Mistletoes often have obligate mutualistic relationships with mistletoe birds, the birds gaining food from the plants, and the parasitic plants gaining seed dispersal to new hosts from the birds (Reid 1991). Recolonisation of Tasmania by mistletoes or mistletoe birds would be extremely difficult even when climatic conditions were suitable for their survival, since the survival of each partner (bird or plant) is dependant on the presence of adults of the other partner.

Extinctions are discussed further in Chapter 7.

Chapter 7 : General Discussion : Community and Vegetation Changes during the Pleistocene in Tasmania

The fossil record implies that plant communities during glacial periods were often floristically different from modern communities. The shrub steppe communities suggested for the last glacial maximum were dominated by a combination of Poaceae, Asteraceae and Chenopodiaceae (e.g. Macphail and Colhoun 1985; Hope 1978). This combination of taxa appears to have been widespread in higher and drier areas of Tasmania. This combination does not occur in modern Tasmania (except possibly in coastal areas from the combination of inputs from salt marsh and dune vegetation) but its occurrence can easily be attributed to the presence of climatic conditions no longer occurring in Tasmania (lowland areas of Eastern Tasmania were probably drier than any part of modern Tasmania, and much of the high altitude areas were almost certainly drier than any alpine area of modern Tasmania).

Communities during interglacial periods, however, also often appear to be composed of combinations of taxa which no longer occur, and for which there is no Holocene record. This is less easily attributed to climatic differences, since climates during previous interglacials are likely to have been similar to Holocene climates. The association of high proportions of Casuarinaceae with rainforest groups provide one strong line of evidence of differences between past and present communities. The fossil record suggests some *Allocasuarina* species, in particular, played different ecological roles during the Pleistocene from extant *Allocasuarina* species. *Allocasuarina* occurs abundantly in most western Tasmanian Pleistocene interglacial or interstadial macrofossil bearing sediments. Correspondingly high levels of Casuarinaceae pollen typify most microfossil deposits of these times (e.g. Hill and Macphail 1985; Colhoun 1988; Colhoun *et al.* 1989; Fitzsimons *et al.* 1990 and Jordan *et al.* 1991). These high levels of both micro- and macrofossils are in association with now typically wet forest taxa, especially *Nothofagus cunninghamii, Lagarostrobos franklinii* and *Phyllocladus asplenifolius.* Casuarinaceae pollen concentrations

have been generally low in sediments since before the Last Glacial maximum, possibly due to an increase in fire frequencies. Similar trends are apparent in records from southeastern mainland Australia except that the decline in *Allocasuarina* may have occurred earlier than in Tasmania (Singh *et al.* 1981). It is likely that *Allocasuarina* species formed a major part of wet forest communities in southeastern Australia, and especially Tasmania, for most of the Pleistocene, at least in riparian communities. *Cyathea* spores are present in many Pleistocene deposits predating the Last Glacial stage including Regatta Point (Hill and Macphail 1985; Macphail pers. comm.), Regency (Fitzsimons *et al.* 1990) and Melaleuca Inlet (Jordan *et al.* 1991). *Cyathea* is now virtually absent from western Tasmania. *Sambucus gaudichaudiana* (which is now restricted in Tasmania to the dry northern parts) pollen occurs in the Melaleuca Inlet sediments.

Even during the Holocene, combinations of taxa which are absent or uncommon in modern vegetation were common in Tasmania (Macphail 1984).

7.1 : Macrofossil Evidence for Vegetation and Community Change

There are indications of significant differences between the vegetation near Regatta Point at the time of deposition of RPU1 and modern vegetation. Extinct rainforest and sclerophyll taxa occur in the sediments (see chapter 6). There are elements of vegetation types which do not now co-occur. Most of the fossil taxa are consistent with modern lowland Tasmanian vegetation. *Rubus* cf. *moorei* forma *glabra*, *Quintinia* species and aff. *Austromyrtus*, however, all have closest affinity with taxa which are now in high altitude rainforests of northern New South Wales/southern Queensland or the rainforests of New Zealand. These are forests with wetter, and possibly warmer, summers than those of modern western Tasmania. In contrast, taxa which are now associated with Tasmanian montane vegetation occur in the sediments. *Podocarpus* cf. *lawrencii* and aff. *Richea milliganii* have affinities with, and are morphologically similar to montane taxa.

It is unlikely that the co-occurrence of taxa with affinities to such diverse modern vegetation types is generally the result of long distance dispersal. If the climate was not much cooler than at present, alpine conditions could have only been present in high altitude areas which would have been distant from the site (see chapter 2). The taxa suggesting cold climate (except *Orites revoluta*) are too common to be the result of long distance dispersal. Only a single leaf of *O. revoluta* has been recovered. Its leaves are good candidates for preservation and probably well transported (Hill and Gibson 1986a) and are distinctive.

Allocasuarina cf. *verticillata* is abundant in the sediments. This taxon was probably a wet forest species which is now extinct, as argued below. The only other reasonable alternative is that two extant species (*A. verticillata* and another species similar to *A. rigida*) were present. Both these species would imply conditions drier than at present.

The morphology of *Nothofagus cunninghamii* reinforces the notion that elements of cold and warm adapted vegetation contributed to the fossil assemblage, since the distribution of leaf lengths is strongly bimodal (see chapter 5). The temperature predictions for two modes are one which is virtually alpine, and one which is as warm as or warmer than modern conditions.

The apparent vegetation anomalies are stronger in RPU2 than in RPU1. Along with taxa consistent with extant lowland riparian vegetation of western Tasmania there are taxa with affinity to modern taxa with strong preferences for different climates. Broad-leaved Lauraceae are now almost exclusively restricted to wet forest of warmer climates than those of present day western Tasmania. The presence of other taxa (e.g. *Rubus* cf. *moorei* forma *glabra* and *Quintinia* species) also suggest warmer conditions than at present. Most of the species closely related to both *Callitris/Actinostrobus* and *Oxylobium* sp. nov. occur only in arid, semi-arid or seasonally dry habitats but *Oxylobium ilicifolium* now occurs on thin siliceous soils in areas of low-moderate rainfall and *C. macleayanus* is a rainforest associate in northern New South Wales and southern Queensland. *C. intratropica* and the New Caledonian species also occur in warm wet areas. The fossil presence of *Callitris/Actinostrobus* could therefore be evidence of either

warm and wet conditions or of dry conditions, and *Oxylobium* sp nov. as evidence of depauperate soils.

A similar array of taxa with preferences for cooler conditions to that found in RPU1 is present. *Microcachrys tetragona* is the most anomalous of these. It is now exclusively alpine (Curtis and Morris 1975). It has a prostrate habit, which is maintained in cultivation at sea-level in Tasmania where it grows well both vegetatively and reproductively. Its prostrate habit decreases the probability of its foliage entering streamways. More than 40 well preserved specimens have been found from all strata of RPU2, so long distance dispersal can be excluded, even though the species has robust leafy stems. It is most likely, therefore, that the *M. tetragona* fossils were derived from lowland sources. Either the fossils were from a morphologically indistinguishable but physiologically different taxon to *M. tetragona*, or *M. tetragona* is capable of competing at low altitudes, though perhaps only under altered atmospheric CO_2 concentration or rainfall regimes.

Changes in atmospheric CO_2 concentration are well documented for the Late Pleistocene (Barrett 1991), and have been predicted for the last 570 million years (Berner 1990). In particular, levels in the Last Interglacial were higher than pre-industrial revolution levels of modern times, and levels during the last two glacials were considerably lower than modern levels (Bartlett 1991). The consequences of elevated or reduced atmospheric CO_2 concentrations on the ecology of wild plants are unknown, but some ~~fertilization~~ interaction is likely (e.g. Beerling and Chaloner 1992). Changes in atmospheric CO_2 concentrations may have played a role in the extinction of any of the taxa discussed here, but there is no corroborative evidence for this.

The vegetation implied by the fossils in the Regency sediments differ from modern communities primarily in the role of *Allocasuarina*. The combination of *Allocasuarina* and *Nothofagus cunninghamii* would be unlikely in modern vegetation.

There are differences between the inferred fossil vegetation at Melaleuca Inlet and extant vegetation. The absence of *Eucalyptus* macrofossils from the Melaleuca Inlet sediments and low representation of

pollen is significant as it indicates that the genus was not as common in the region as it is today. Its pollen is well represented in modern samples from a variety of vegetation types (Colhoun and van der Geer 1986) and can be transported over long distances (e.g. Hill and Macphail 1985).

Banksia marginata is common in the Melaleuca Inlet region today but has not been recovered from the deposit, whereas the extinct *B. kingii* is common. The highly sclerophyllous leaves of *B. marginata*, its presence in the two litter samples and the abundance of *Banksia* -like species in many Tertiary fossil deposits (Cookson and Duigan 1950; Hill and Christophel 1988) all suggest that *B. marginata* is likely to fossilize well, although it has no fossil record. Its absence from the deposit indicates that it was rare or absent in streambank vegetation at the time of deposition.

Allocasuarina zephyrea is the dominant macrofossil taxon in the deposit, but was not found in extant litter samples and is now uncommon along riverbanks in south-west Tasmania. This suggests that, at the time of deposition of the Melaleuca sediments, *A. zephyrea* formed a major component of the vegetation of the area at least along riverbanks. The combination of very high levels of *Phyllocladus aspleniifolius*, *Lagarostrobos franklinii* and Casuarinaceae pollen with low levels of *Nothofagus cunninghamii* pollen is unknown since the Last Glacial Maximum and is very unlikely to occur in modern vegetation. *Phyllocladus aspleniifolius* and *L. franklinii* now rarely, if ever, co-dominate vegetation without *N. cunninghamii* being abundant, at least nearby, and they are never co-dominant with Casuarinaceae. Macrofossils and microfossils from most other known Pleistocene macrofossil localities in western Tasmania also show high proportions of *Allocasuarina* associated with high levels of some combination of *L. franklinii*, *N. cunninghamii* and/or *P. aspleniifolius*. Macro- and microfossils from most other known Tasmanian Pleistocene macrofossil bearing sediments also show high proportions of *Allocasuarina* with species now typical of rainforest, and these associations are unlike any now known (e.g. Regency and Regatta Point). In addition the Regatta Point *Allocasuarina* species is likely to be nextinct now. It is, therefore, likely that *Allocasuarina* formed associations with species that are now typical of rainforest, and these associations are unlike any now

known.

The role of fire in the evolution and current structure of Tasmanian vegetation is the subject of continuing debate. The Melaleuca sediments contain evidence for the occurrence of local fire in the form of burnt plant organs, and the assemblage is composed of numerous elements which today are regarded as dominants of pyrogenic communities (Jackson 1979). Further, there are burnt remains of rainforest species such as *Lagarostrobos franklinii*, which is recognised as being fire sensitive (Gibson 1986). Burnt macrofossils of the fire sensitive *Athrotaxis cuppressoides* occur in the Late Pleistocene Newton Creek sediments (R. S. Hill pers. comm.). Charcoal occurs during glacial and interstadial periods in the Darwin Crater core at least as far down as 20 m (probably of the order of 200,000 B.P.) (Colhoun, 1988). It is possible that the macrofossil assemblage reflects the result of many ~~modern~~ fires ~~in the~~ like western Tasmania, where the perimeters of patches of rainforest are burnt, and other fires are common. The presence of fire and the abundance of sedgeland-heath and wet scrub suggested by the Melaleuca Inlet fossils is of considerable interest. If the deposit was laid down before human occupation of Tasmania lightning must have been the ignition source for the fires, in spite of the wet climate apparently present at the time. Either low fire frequency regimes maintained by lightning were sufficient to maintain sedgeland-heath and wet scrub forest communities, or lightning provided much higher fire frequencies than is often considered possible. Another possibility is that Aborigines may have been present in Tasmania early enough to create well established fire dependent communities at the time of deposition. The minimum age for the Melaleuca Inlet sediments predates the earliest known human presence in Tasmania by about 10,000 years (Cosgrove 1989). Alternatively, it is possible that fires were very infrequent and that the presence of these sclerophyllous communities was a direct consequence of extremely oligotrophic conditions, which may have been exacerbated by the leaching effects of very high rainfalls. As discussed in chapter 2, fire has been a component of Tasmanian ecosystems since at least the Early Pleistocene.

7.2 : Non-equilibrium Ecology of Tasmanian rainforest

Extant taxa must be either recently evolved or adapted or have survived the large climatic fluctuations of the Pleistocene. Survival can only be the result of some combination of breadth of tolerance and ability to disperse to favourable climates. This combination will vary from taxon to taxon, but trends should be apparent under different historical and geographical regimes. Taxa with broad tolerance are less likely to be well dispersed under the competitor/stress tolerator/ruderal strategy model of Grime (1979). Dispersal ability is favoured for ruderal strategies, e.g. early successional plants. Breadth of ecological tolerance is more likely to be favoured by stress tolerator and competitor strategies. A model for Tasmania is that the Tasmanian lowland rainforest taxa survived the Pleistocene climate fluctuations by using broad ecological tolerance rather than dispersal ability for the taxa which have survived the Pleistocene climate fluctuations. Firstly, rainforest taxa are in general close to the stress tolerator and/or competitor end of the continuum. Secondly, almost all the Tasmanian lowland rainforest taxa have very broad ecological tolerances (most live in very wide ranges of climatic environments). Thirdly, fossils of almost all modern Tasmanian lowland rainforest taxa likely to be fossilized occur in the Regatta Point sediments, in the Early Pleistocene, and appear to be little changed morphologically since then. Fourthly, the geography of Tasmania would have favoured rainforest taxa of broad tolerance, rather than those with good dispersal. As argued in chapters 2 and 6 rainforest taxa in Tasmania would have been relatively isolated by large areas of arid/semi-arid country from other areas of rainforest habitat during glacials, and isolated by water during interglacials. Hence, taxa using the dispersal strategy to survive the climatic fluctuations would have required very long distance dispersal to survive, but few rainforest taxa are extremely well dispersed. Finally, western Tasmania would have provided some relatively mesic environments for rainforest during the glacials, due to the presence of mountains generating orographic rain from the probable westerlies.

This model is consistent with the pollen based models of McGlone (1985) who proposed that rainforest taxa survived the glacial-interglacial cycles of the Pleistocene in New Zealand primarily by contracting to and

expanding from numerous small pockets throughout their modern range. This model contrasts with North America and Europe where forest taxa apparently survived mainly by major moves in distribution (e.g. Schoonmaker and Foster 1991).The significant differences between Tasmania (and New Zealand) and these Northern Hemisphere forests are geographical. Tasmania has a strong maritime influence, and western Tasmania (and western New Zealand) is likely to have been less prone to extremely cold winters during the glacials than most of Europe and North America. In contrast to the virtually impassable Bass Strait/semi-arid Bassian Plain barrier of Tasmania, it appears that most forest in North America and Europe had dispersal corridors around or between major georaphical barriers (primarily mountain ranges). Because of these conditions a strategy with higher dispersal rates, rather than breadth of tolerance would have been favoured in these northern hemisphere forests.

An important corollary of this model is that if the rainforest species are poorly dispersed and have broad ecological tolerance then there should be considerable ecological inertia in rainforest vegetation. This is supported by the results in chapter 5 for *Nothofagus cunninghamii*, which is a species with poor dispersal and wide ecological range (extending from alpine shrubberies to lowland forest, and from the wettest parts of Tasmania to the drier rainforest with about 700 mm annual rainfall). The ecological inertia of other rainforest taxa in Tasmania is open for further research. A corollary of high ecological inertia is that the distribution of taxa should have a strong historical component. This has been argued for Tasmanian rainforest by Macphail (1979), Kirkpatrick and Brown (1984 a & b), Noble (1986) and Hill and Read (1987), and in chapter 5. A test of this hypothesis is related to taxa which became extinct in the Early or Middle Pleistocene. The model predicts that these taxa have relatively narrow ecological tolerances, and may be well dispersed. Arguments based on the ecology of modern closest relatives are limited in power since these modern taxa are also likely to have passed through severe climatic filters in the Pleistocene, but some inferences can be made. Of the extinct rainforest taxa which occur in the Linda Valley most have closest modern relatives only in forest which is less prone to summer drought than western Tasmania (see chapter 6), though

there is little evidence for narrow temperature ranges for these taxa. However, several of the taxa are likely to have been well dispersed compared with modern Tasmanian rainforest taxa (especially the fleshy fruited *Laurophyllum*, *Dacrycarpus/Dacrydium* and aff. *Austromyrtus*). Further testing of these hypotheses may involve autecological studies of the relevant taxa, and particularly pollen studies from the Bass Strait area from the Last Interglacial and before.

These arguments do not apply as well to the non-rainforest vegetation of Tasmania. Wet sclerophyll vegetation is largely an early seral community type, and the taxa involved are generally well dispersed. The Bassian Plain would have provided a less serious barrier to the dispersal of drier vegetation types (e.g. dry sclerophyll).

Another consequence of the survival of taxa with broad ecological tolerance is that they are likely to expand their realised niches to fill the niches vacated by extinctions. This was argued for *Banksia marginata* and other sclerophyll taxa in chapter 6, but is likely to apply to rainforest taxa.

7.3 : Summary of Changes in Vegetation

Some stages are apparent in the record of community change in western Tasmania during the Pleistocene :

(1) Early Pleistocene lowland rainforest was more diverse than modern rainforest. A number of now extinct species were present. Many of the extinct species were rainforest taxa which probably had persisted from a diverse Tertiary rainforest flora. Others were sclerophyll species. Otherwise, communities during interglacials were probably structurally similar to modern communities. *Eucalyptus* spp. and fire were present, but probably were uncommon, at least in riparian communities. *Allocasuarina* was abundant in riparian communities.

(2) Glacial periods with different vegetation undoubtedly occurred in the Early Pleistocene, but are not known from the fossil record.

(3) By some time in the Middle Pleistocene almost all of the now extinct taxa had probably disappeared from, or become rare in, western Tasmania. *Allocasuarina* remained abundant in riparian communities, and possibly elsewhere and probably formed 'mixed forest' communities with

various rainforest and sclerophyll types analogous to modern *Eucalyptus*/rainforest mixed forest communities. *Eucalyptus* and fire remained uncommon.

(4) Transition periods from glacial to interglacial conditions were often characterised by a transition from sclerophyll to rainforest dominated vegetation.

(5) Some time during the Middle or Late Pleistocene the wet scrub, and the wet sclerophyll communities now typical of western Tasmania probably became more common as interglacial vegetation. If the vegetation indicated by the Melaleuca Inlet sediments, and the Langdon River sediments (Colhoun *et al.* 1989) were more or less normal for western Tasmania this preceded the apparent replacement of *Allocasuarina* by *Eucalyptus*. The increase in fire frequency, and the changes from vegetation which was apparently adapted infrequent fires to vegetation adapted to high fire frequency seems to have been gradual.

(6) Much of upland Tasmania apparently carried shrub steppe dominated by Poaceae, Asteraceae and Chenopodiaceae during the last glacial maximum, with various combinations of rainforest and sclerophyll vegetation in the stages leading up to and down from this maximum.

(7) Rainforest taxa are particularly likely to have been more or less out of equilibrium with climate at most stages of the Pleistocene.

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Appendix 1 : Taxonomic authorities

Species	Authority
Acacia koaia	Hillebr.
A. melanoxylon	R. Br.
A. mucronata	Willd. ex H. Wendl.
A. sophorae	(Labill.) R. Br. ex Ait.
Acmena smithii	(Poiret) Merr. & Perry
Acradenia eodiiformis	(F. v. M.) T. Hartley
A. frankliniae	Milligan ex Kippist
Actinostrobus arenarius	Gardner
A. pyramidalis	Miq. in Lamb
Agastachys odorata	R. Br.
Allocasuarina huegeliana	(Miq.) L. Johnson
A. littoralis	(Salisb.) L. Johnson
A. monilifera	(L. Johnson) L. Johnson
A. rigida	(Miq.) L. Johnson
A. verticillata	(Lam.) L. Johnson
A. zephyrea	Wilson & Johnson
Anodopetalum biglandulosum	A. Cunn. ex Hook. f.
Anopterus glandulosus	Labill.
A. macleayanus	F. v. M.
Archeria eriocarpa	Hook. f.
A. hirtella	(Hook. f.) Hook. f.
A. serpyllifolia	(Hook.f.)
Aristotelia peduncularis	(Labill.) Hook. f.
Asplenium bulbiferum	Forst. f.
Astelia alpina	R. Br.
Atherosperma moschatum	Labill.
Athrotaxis cupressoides	D. Don
A. laxifolia	Hook.
A. selaginoides	D. Don
Austromyrtus dallachianus	(Benth.) L. S. Smith
A. lasiocladus	(F. v. M.) L. S. Smith
Baeckia gunniana	Schauer
Banksia aemula	R. Br.
B. brownii	Baxter ex R. Br.
B. canei	J. H. Willis
B. conferta	A. S. George
B. dryandroides	Baxter ex Sweet
B. ericifolia	L. f.
B. grossa	A. S. George
B. incana	A. S. George
B. integrifolia	L. f.
B. integrifolia var compar	(R. Br.) Bailey
B. kingii	Jordan & Hill
B. lanata	A. S. George
B. laricina	C. Gardner
B. leptophylla	A. S. George
B. littoralis	R. Br.
B. marginata	Cav.
Banksia meisneri	Lehm.

Appendix 1 (cont.)

Species	Authority
B. micrantha	A. S. George
B. nutans	R. Br.
B. oblongifolia	Cav.
B. occidentalis	R. Br.
B. paludosa	R. Br.
B. plagiocarpa	A. S. George
B. pulchella	R. Br.
B. robur	Cav.
B. saxicola	A. S. George
B. scabrella	A. S. George
B. seminuda	(A. S. George) B. Rye
B. serrata	L. f.
B. sphaerocarpa	A. S. George
B. spinulosa	Smith
B. spinulosa var. cunninghamii	(Siber ex Reichenbach) A. S. George
B. spinulosa var. neoanglica	A. S. George
B. strahanensis	Jordan & Hill
B. telmatiaea	A. S. George
B. tricuspis	Meissner
B. verticillata	R. Br.
B. violaceae	C. Gardner
Barbella nitens	(Hook.f. et Wils.) Nog.
Bauera rubioides	Andr.
Bellendena montana	R. Br.
Bryum argenteum	Hedw.
Callitris baileyi	C. T. White
C. drummondii	(Parl.) F. v. M.
C. intratropica	F. v. M.
C. macleayana	F. v. M.
C. rhomboidea	R. Br. ex A. & L. Rich.
C. roei	F. v. M.
C. sulcata	(Parlat) Schlecter
Calorophus elongatus	Labill.
Cassinia aculeata	R. Br.
Cenarrhenes nitida	Labill.
Clematis aristata	R. Br. ex DC.
Coprosma nitida	Hook.f.
C. quadrifida	(Labill.) Robinson
Cryptocarya novae-anglica	B. Hyland & Floyd
Cyathodes juniperina	(Forst.) Druce
C. parvifolia	R. Br.
Dacrycarpus dacrydioides	(A. Rich.) de Laubenf.
D. eocenica	D. R. Greenwood
D. praecupressinus	(Ett.) D. R. Greenwood
Dacrydium cuppressinum	Soland. ex Lamb.
Dicksonia antarctica	Labill.
Diselma archeri	Hook.f.
Donatia novae-zelandiae	Hook. f.
Dracophyllum milliganii	Hook. f.

Appendix 1 (cont.)

Species	Authority
Embothrium concinnum	J. R. & G. Forst.
Epacris heteronema	Labill.
E. impressa	Labill.
E. lanuginosum	Labill.
E. mucronulata	R. Br.
Eucalyptus nitida	Hook. f.
E. regnans	F. v. M.
E. subcrenulata	Maiden & Blakely
Eucryphia cordifolia	Cav.
E. glutinosa	(Prepp. et Endl.) Baill.
E. lucida	(Labill.) Baill.]
E. milliganii	Hook. f.
E. moorei	F. Muell.
Gahnia grandis	(Labill.) S. T. Blake
Gastrolobium spinosum var trilobum	Benth.
Gaultheria hispida	R. Br.
Gleichenia dicarpa	R. Br.
Gothanipollis perplexus	Pocknall & Mildenhall
Grimmia trichophylla	Grev.
Gymnoschoenus sphaerocephalus	(R. Br.) Hook. f.
Hakea lissosperma	R. Br.
H. nodosa	R. Br.
Hynum cupressiformis	Hedw.
Lagarostrobos franklinii	(Hook. f.) Quinn
Lembophyllum divulsum	(Hook. f & Wils.) Par.
Leptospermum glaucescens	S. Schauer
L. nitidum	Hook. f.
L. riparium	D. I. Morris
L. scoparium	Forst. & Forst. f.
Lomatia arborescens	L. Fraser & Vick.
L. dentata	R. Br.
L. ferruginea	R. Br.
L. ilicifolia	R. Br.
L. tasmanica	W. M. Curtis
L. tinctoria	R. Br.
Lycopodium laterale	R. Br.
Matonisporites ornamentalis	(Cookson) Partridge
Melaleuca squameum	Labill.
Melaleuca squarrosa	Donn ex Smith
Microcachrys tetragona	(Hook.) Hook. f.
Microsorum diversifolium	(Willd.) Copel.
Microstrobos niphophilus	Garden and Johnson
Mirbelia dilatata	R. Br.
Myrtacidites verrucosus	Partridge
Monotoca glauca	(Labill.) Druce
M. submutica	(Benth.) Jarman
Nemcia triloba	(Meissner) Crisp
Notelaea ligustrina	Vent.
Nothofagus cunninghamii	(Hook.) Oersted

Appendix 1 (cont.)

Species	Authority
Nothofagus moorei	(F. Muell.) Krasser
N. gunnii	(Hook. f.) Oerst.
Olearia ledifolia	(DC.) Benth.
O. persooniodes	(DC.) Benth.
Orites diversifolia	R. Br.
O. milliganii	Meisn. in Hook
O. revoluta	R. Br.
Oxylobium ilicifolium	(Andr.) Domin
O. staurophyllum	(DC.) Benth.
Pappilaria crocea	(Hampe) Jaeg.
Phebalium squameum	(Labill.) Engler
Phyllocladus alpinus	Hook. f.
P. aspleniifolius	(Labill.) Hook. f.
Pimelea cinerea	R. Br.
P. drupacea	Labill.
Pittosporum bicolor	Hook.
Podocarpus lawrencii	Hook. f. in Hook.
Polytrichadelphus magellanicus	(Hedw.) Mitt.
Polyytrichum juniperinum	Hedw.
Pomaderris apetala	Labill.
Prionotes cerinthoides	(Labill.) R. Br.
Ptychomnion aciculare	(Brid.) Mitt.
Quintinia acutifolia	Kirk
Q. psilatispora	Martin
Q. sieberi	A. DC
Richea acerosa	(Lindley) F.v. M.
R. milliganii	(Hook.f.) F. v. M.
R. pandanifolia	Hook. f.
R. scoparia	Hook. f.
Rubus cissoides	A. Cunn.
Rubus fraxinifolius	Poiret
Rubus gunnianus	Hook.
Rubus moorei	F. v. M.
Rubus parvifolius	L.
Rubus primaevis	Frenguelli
Sambucus gaudichaudiana	DC.
Sprengelia incarnata	Smith
Stepanocolpites oblatus	Martin
Symplocoipollenites austellus	Partridge
Tasmannia lanceolata	(Poiret) A. C. Smith
Telopea mongaensis	Cheel
T. oreades	F. v. M.
T. speciossissima	(Smith) R. Br.
T. truncata	(Labill.) R. Br.
Tetracarpaea tasmanica	Hook. f.
Thuidium furfurosum	(Hook. f. & Wils.) Sains.
T. laevisculum	(Mitt.) Jaeg.
Trachyloma diversinerve	Hampe in F. v. M.
T. planifolium	(Hedw.) Brid.

Appendix 1 (cont.)

Species	Authority
Trochocarpa cunninghamii	(DC.) W. M. Curtis
T. disticha	(R. Br.) Spreng.
T. gunnii	(Hook. f.) Benth.
Tubulifloridites pleistocenicus	Martin
Weymouthia cochlearifolia	(Schwaegr.) Dix.
W. mollis	(Hedw.) Broth.

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Two New *Banksia* Species from Pleistocene Sediments in Western Tasmania

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Abstract

Subtribe *Banksiinae* of the Proteaceae was diverse in Tasmania in the early and middle Tertiary, but is now restricted to two species, *Banksia marginata* and *B. serrata*. Rapid and extreme environmental changes during the Pleistocene are likely causes of the extinction of some *Banksia* species in Tasmania. Such extinctions may have been common in many taxonomic groups. The leaves and infructescences of *Banksia kingii* Jordan & Hill, sp. nov. are described from late Pleistocene sediments. This is the most recent macrofossil record of a now extinct species in Tasmania. *Banksia kingii* is related to the extant *B. saxicola*. *Banksia strahanensis* Jordan & Hill, sp. nov. (known only from a leaf and leaf fragments and related to *B. spinulosa*) is described from Early to Middle Pleistocene sediments in Tasmania. This represents the third Pleistocene macrofossil record of a plant species which is now extinct in Tasmania.

Introduction

Only two extant species of *Banksia* occur naturally on mainland Tasmania. *Banksia marginata* Cav. is widespread and *B. serrata* L. f. is restricted to a small area of north-west Tasmania (Taylor and Hopper 1988). However, three species of *Banksieaephyllum* Cookson & Duigan and one species of *Banksieaeformis* Hill & Christophel have been described from Eocene and Oligocene sediments in Tasmania (Hill and Christophel 1988). Also, four undescribed species of *Banksieaephyllum* and two of *Banksieaeformis* have been recovered from the Oligocene Cethana sediments, although one of the species of *Banksieaeformis* may be the same as one of the species of *Banksieaephyllum* (Carpenter, unpublished data). These taxa cover a wide range of forms and their affinities at the subgeneric level are uncertain. *Banksieaephyllum* encompasses organically preserved fossil leaves consistent with the subtribe Banksiinae. Banksiinae encompasses the extant genera *Banksia*, now widespread in Australia, and *Dryandra*, now restricted to south-western Western Australia (Cookson and Duigan 1950). *Banksieaeformis* is used to describe leaves with architecture consistent with Banksiinae but without cuticular preservation (Hill and Christophel 1988). There are no Tasmanian Miocene or Pliocene macrofossil records of the subtribe Banksiinae, but there is a paucity of macrofossil-bearing sediments of these ages. It is clear that there were many kinds of *Banksia* or close relatives in Tasmania in the early Tertiary and that almost all are now extinct, but it is not clear when these extinctions occurred.

Kirkpatrick and Brown (1984: 180) suggest that rapid climatic changes of the initial Pleistocene glacial cycles 'must have seen a flurry of extinction and speciation in Tasmania'. Dramatic climatic and landform changes occurred during the Pleistocene in

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Tasmania. Although there is now no permanent ice in Tasmania, it was glaciated to low altitudes for at least three periods in the Pleistocene (Colhoun 1985). Shackleton and Opdyke (1973) used oxygen isotope analysis to demonstrate roughly cyclic variation in deep sea temperatures, with perhaps six periods since 800 000 years ago as cold as or colder than the last glaciation interspersed with periods as warm or nearly as warm as today. There have been rapid and large temperature changes since about the Plio-Pleistocene boundary (Shackleton 1984). It is likely that during the coldest parts of the Pleistocene the climate was drier than at present, although perhaps less so in western Tasmania (Sigleo and Colhoun 1981).

There has been human occupation of Tasmania for at least 30 000 years (Cosgrove 1989). Jackson (1965) proposed that increased fire frequencies were associated with human activity and that this caused major changes in the vegetation of Tasmania.

The Pleistocene was therefore a period during which many plant extinctions may have occurred. There is, however, relatively little fossil evidence of plant extinctions during the Pleistocene in Tasmania. Latest Pliocene/early Pleistocene sediments at Linda Valley contain pollen of *Beauprea*, *Nothofagus* subgen. *Brassospora*, *Ascarina* and *Dacrydium* s. str. which are extinct in Australia, and of Araucariaceae and *Quintinia* which are extinct in Tasmania (Hill and Macphail, in press). All these taxa have distinctive pollen. The early–middle Pleistocene Regatta Point sediments contain pollen and spores of extinct taxa, but it is likely that reworking of pollen from Tertiary sediments has occurred (Hill and Macphail 1985, in press).

Fossil palynomorphs tend to have low taxonomic resolution and hence it is often not possible to determine their living affinities with precision. Many extinctions may therefore be masked in the microfossil record by this lack of resolution. Macrofossils can often be identified with higher taxonomic resolution than palynomorphs and thus hold the potential for the identification of extinctions not apparent in the fossil palynomorph record.

However, apart from the two species of *Banksia* described here, there is only one Pleistocene plant macrofossil record of a species which is now extinct in Tasmania: *Quintinia* cuticle from Regatta Point (Hill and Macphail 1985). The scarcity of records is probably because few studies have been made of Tasmanian Pleistocene plant macrofossils.

Banksia pollen occurred throughout the Pleistocene, e.g. in the late Pliocene–early Pleistocene Linda Valley sediments (Hill and Macphail, in press), the mid-Pleistocene Regency sediments (Fitzsimons *et al.* 1990) and the late Pleistocene Tullarbardine Dam sediments (Colhoun and van der Geer 1986). The *Banksia* pollen taxa described in these deposits are consistent with extant Tasmanian species, but cannot always be discriminated from some closely related *Banksia* species, particularly in older deposits, often because of deterioration (M. K. Macphail, personal communication). *Banksia* species may therefore have persisted into the Pleistocene and then become extinct, possibly due to the rapid climatic changes of this period or to activities of Aborigines. This paper describes two, now extinct Pleistocene *Banksia* species.

Materials and Methods

The Fossil Sites

(1) Regatta Point

A leaf and several leaf fragments of *Banksia* were extracted from sediments at Regatta Point. These sediments are described in Hill and Macphail (1985) as being of late Pliocene/early Pleistocene age. A recent re-examination has refined the date to early to middle Pleistocene (Hill and Macphail, in press).

(2) Melaleuca Inlet

Banksia leaves, infructescences and numerous other leaf and wood fossils were extracted from mine workings of C. D. (Denny) King in alluvial sediments at Melaleuca Inlet. The sediments have been

moved by Denny King's mining and their stratigraphy cannot be determined. However, the leaves were derived from a single sedimentary lens and the infructescences from a separate lens nearby (C. D. King, personal communication). The sediments are composed of large, water-rounded quartz and schist fragments and are probably derived from a high-energy river system.

Coniferous wood from the lens containing leaves has been ^{14}C dated at 38 800 ± 1 300 B.P. (S.U.A. 5038). Part of a fossil *Banksia* infructescence has been dated at 34 000 ± 500 B.P. (S.U.A. 2947) by accelerator mass spectrometry after reduction to cellulose. Colhoun (1986) showed that older ^{14}C dates from western Tasmania can significantly underestimate the age of the deposits due to contamination by younger, and hence ^{14}C enriched, organic material present in soil water. ^{14}C ages should therefore be treated as minimum ages. Palynological evidence from the lens that contained the leaves is consistent with an interstadial climate possibly from the last glaciation (M. K. Macphail, personal communication). The ^{14}C ages of the two lenses are well within the range of finite dating and are similar, and it is therefore likely that they are of similar true age. The Melaleuca Inlet deposit is therefore at least 34 000 years old and probably from an interstadial period of the last or second last glaciation.

Methods.

Macrofossils were extracted by gently macerating the sediments in warm water containing about 5% hydrogen peroxide. To prepare cuticles, leaf fragments were placed in 10% aqueous chromium trioxide and kept warm until all non-cuticular organic material had oxidised. The cuticles were then neutralised with 5% aqueous ammonia, stained with 1% safranin O and mounted on slides in phenol glycerine jelly. Thick and thin sections were cut using a freeze microtome. Thick sections were mounted on double-sided adhesive tape on slides and air-dried. Thin sections were mounted on slides in phenol glycerol jelly. Cuticles and thin sections were photographed under transmitted light and thick sections under reflected light with a Zeiss Axiophot photomicroscope. Small leaves were photographed with a Wild M5 microscope and large specimens with an Olympus OM series 35-mm camera with macro lens and bellows or a Pentax 6 × 7 cm camera with bellows.

Fossils were compared with a wide range of extant material of tribe Banksieae including *Musgravea*, *Austromuellera*, all species of *Banksia* and most species of *Dryandra*. This included specimens covering a wide range of the variation within species closely allied to the fossil taxa. Taxonomy follows George (1981) and Johnson and Briggs (1975).

Banksia kingii sp. nov. fossils were found in sediments at Melaleuca Inlet, south-western Tasmania and *B. strahanensis* sp. nov. fossils in sediments at Regatta Point, western Tasmania (Fig. 1). *Banksia strahanensis* is included in Hill and Macphail (1985) as a species of unknown affinity.

Systematics

Family: Proteaceae
Subfamily: Grevilleoideae
Tribe: Banksieae
Banksia L.f.
Subgenus: *Banksia*
Section: *Oncostylis* Benth.
Series: *Spicigerae* A. S. George
Banksia strahanensis Jordan & Hill, sp. nov.

Diagnosis

Leaf linear, bifacial, entire, obtuse and mucronate, 2–3 mm wide, about 40 mm long, petiole 3·5–4 mm long, margins thick and revolute, non-stomatiferous surface sparsely hairy, stomatiferous surface with prominent midrib, lamina between margin and midrib exposed and densely hairy. Cuticle of non-stomatiferous surface with roughly isodiametric cells without papillae or ribbing, 1–3 celled trichome bases of rounded, slightly enlarged cells present. Cuticle of stomatiferous surface with lamina between midrib and each margin uniformly composed of superficial stomates evenly interspersed with rhomboidal cells bearing single trichome bases and with porose cell walls except near the margins and midrib, where all cells bear single trichome bases. Cuticle of midrib of elongate, thick-walled cells with occasional 1–2-celled trichome bases.

Location: Early–Middle Pleistocene sediments, Regatta Point, western Tasmania.

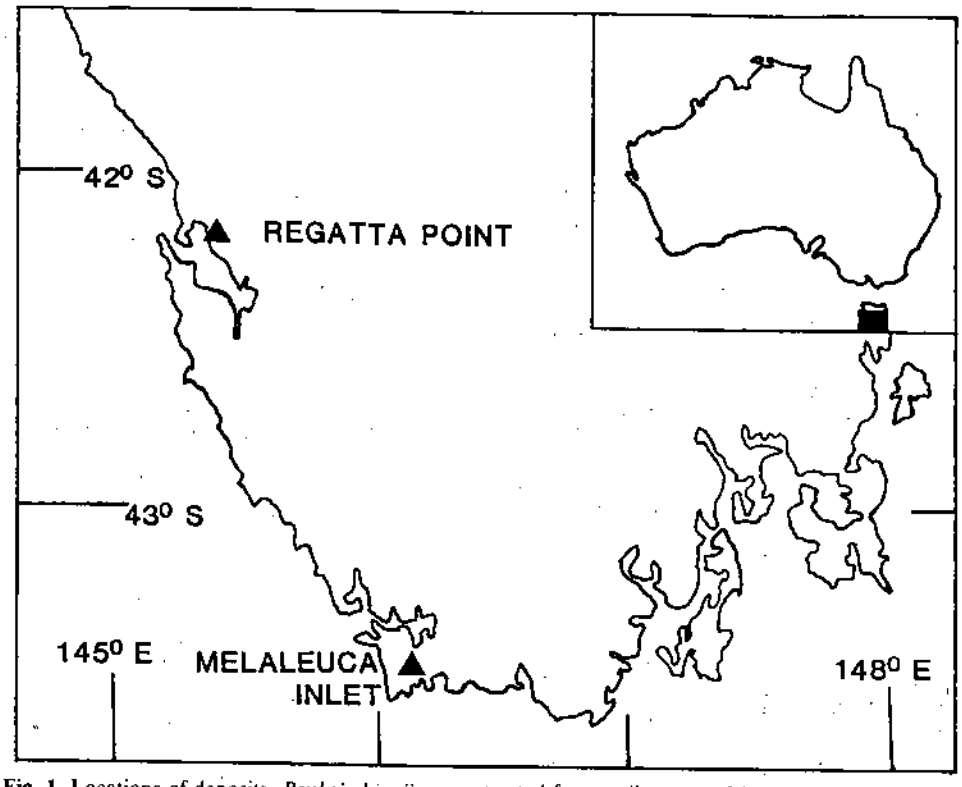


Fig. 1. Locations of deposits. *Banksia kingii* was extracted from sediments at Melaleuca Inlet. *Banksia strahanensis* was extracted from sediments at Regatta Point.

Holotype: RPU-381, stored in the Department of Plant Science, University of Tasmania.

Etymology: From the town of Strahan near Regatta Point.

Specimens Examined

RPU-022 to RPU-025, RPU-380, RPU-381 and RPU-405–RPU-408 stored in the Department of Plant Science, University of Tasmania. Hill and Macphail (1985) refer to RPU-023 and RPU-024 as RP-077 and RP-078. The numbering system for these fossils has been changed to distinguish specimens from Pleistocene sediments from those in underlying Eocene sediments.

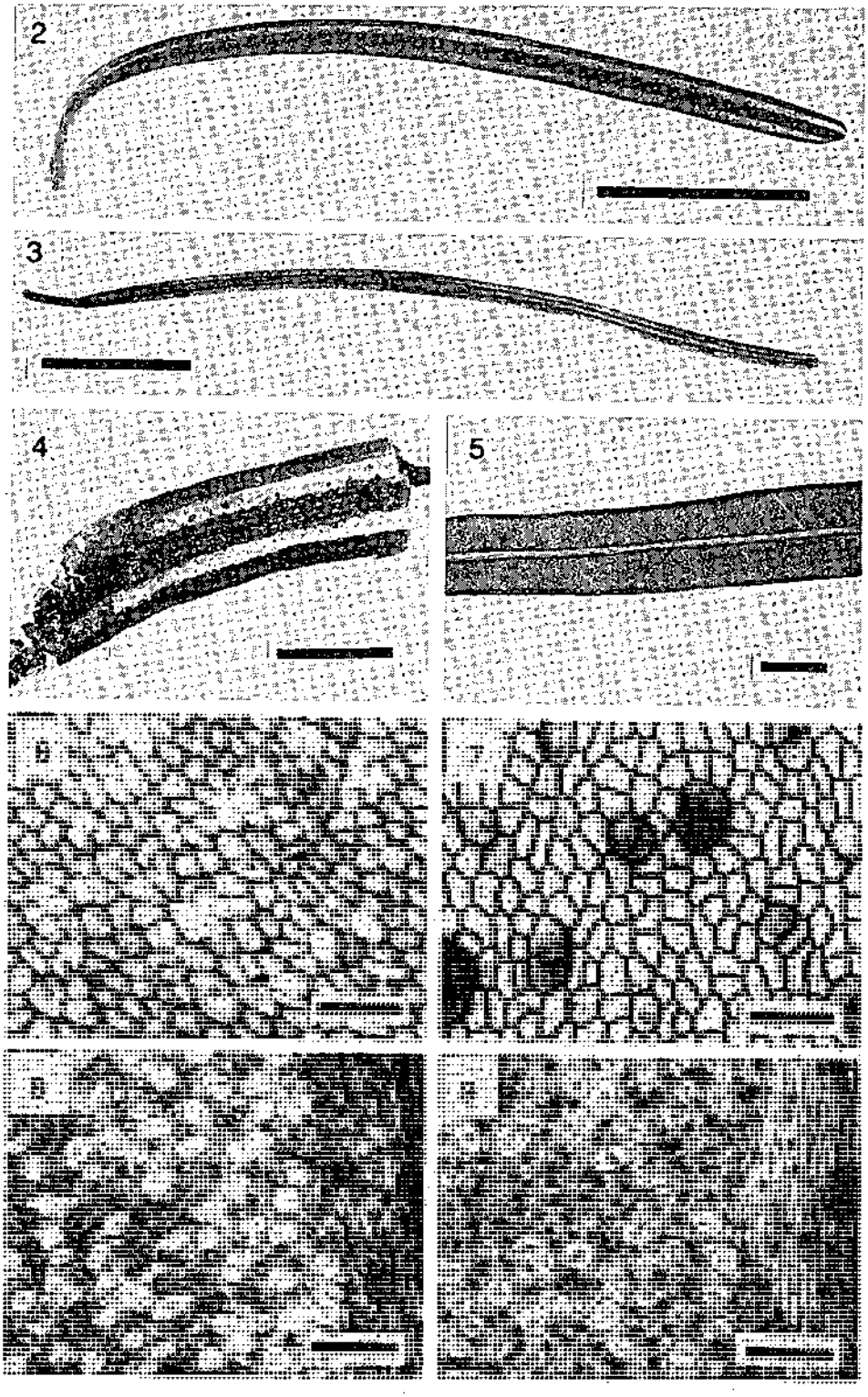
Discussion

Banksia strahanensis is illustrated in Figs 2, 4, 6 and 8, and *B. spinulosa* Smith is illustrated for comparison in Figs 3, 5, 7 and 9. The cuticular and leaf morphology of the fossil place it readily in subtribe Banksiinae. Very narrow, entire leaves and the absence of apparent reticulate venation on the stomatiferous surface occur only in section *Oncostylis* of *Banksia* (George 1981) and do not occur in *Dryandra*. *Banksia strahanensis* is compared with all the extant members of *Oncostylis* in Table 1, which includes taxonomic authorities. Section *Oncostylis* is composed of three series: *Spicigerae*, which includes *B. spinulosa* and *B. ericifolia* from south-eastern Australia and other species all from south-western Western Australia, and series *Abietinae* and *Dryandroideae*, which are restricted to south-western Western Australia. *B. strahanensis* is clearly a member of series *Spicigerae*. Series *Dryandroideae*, which contains only *B. dryandroides*, differs in having leaves with deep triangular lobes. Cuticular ribs connecting hair bases on the outer surface of the cuticle of the non-stomatiferous surface are highly distinctive features of *B. tricuspis* and some species of series *Abietinae*. Series

Table 1. Leaf and cuticle morphological characters of species of *Banksia* section *Oncostylis* Benth. including *B. strahanensis* Jordan & Hill, sp. nov.

The information in this table is derived from this study and George (1981). In the column 'margin shape', entire means the leaf margin is entire for most of its length. In the column 'revolute margin', – means recurved margin, + means revolute margin, ++ means strongly revolute margin. In other columns, + means present, – means absent, (+) means present but poorly developed and ± means more or less, or either present or absent. In the column 'cell size', small is mean cell width <35 μm, large is mean cell width >45 μm. In the column 'cell length', short is mean cell length : mean cell width <1·5 : 1, long is mean cell length : width >1·5 : 1

Species	Leaf form characters							Cuticle characters					
								Non-Stomatiferous surface			Stomatiferous surface		
	Leaf shape	Margin shape	Revolute margin	Leaf width (mm)	Leaf length (cm)	Petiole length (mm)	Apex shape	Papillae	Cell size	Cell shape	Lamina hairs	Veins	Ribs
B. strahanensis Jordan & Hill	linear	entire	+	2–2·5	4	3·5–4	obtuse	–	small	long	dense	–	–
Series *Spicigerae* A. S. George													
B. spinulosa Smith	linear	±serrate	±	1·5–11	3–11	1–3	±obtuse	±	small	long	dense	+	–
B. ericifolia L.f.	linear	entire	++	0·8–1·5	0·9–2	1–2	3-toothed	+	small	long	dense	+	–
B. brownii Baxter ex R. Br.	elliptic	lobed	+	3–5	3–11	2–5	retuse	+	large	long	dense	+	–
B. occidentalis R. Br.	linear	±serrate	+	2–3	4–13	1–5	truncate	+	large	short	dense	+	–
B. littoralis R. Br.	linear	entire	–	4–10	10–23	5–10	±obtuse	+	small	long	dense	+	–
B. seminuda (A. S. George) B. Rye	linear	entire	–	4–18	5–12	5–10	±obtuse	+	small	long	dense	+	–
B. tricuspis Meissner	linear	entire	++	1–1·5	5–13	2–5	obtuse	–	small	short	+	+	+
B. verticillata R. Br.	elliptic	±serrate	–	·7–12	3–9	5–11	obtuse	+	large	short	dense	+	–
Series *Abietinae* Meissner													
B. nutans R. Br.	linear	entire	++	0·5–1·3	1–2·8	2–3	acute	+	large	long	+	+	–
B. grossa A. S. George	linear	entire	++	1·8–2·8	4–12	3–5	obtuse	+	small	short	absent	+	+
B. incana A. S. George	linear	entire	++	1·5–2	1–6	1–2	acute	+	small	short	+	+	(+)
B. lanata A. S. George	linear	entire	++	0·7–1	3–10	3–4	acute	+	small	short	+	+	–
B. laricina C. Gardner	linear	entire	++	±0·8	0·5–1·5	1–1·5	acute	+	small	short	+	+	+
B. leptophylla A. S. George	linear	entire	++	1–1·5	4–10	1–2	acute	±	small	short	+	+	(+)
B. meisneri Lehm.	linear	entire	++	1–1·5	0·3–1·5	0·5–1	obtuse	–	small	short	+	+	–
B. micrantha A. S. George	linear	entire	++	1–1·5	1–3	2–3	acute	+	small	short	absent	+	–
B. pulchella R. Br.	linear	entire	++	1–1·5	0·4–1·3	1–1·5	obtuse	+	small	short	+	+	+
B. scabrella A. S. George	linear	entire	++	±1	0·8–3	1–2	acute	+	small	short	dense	+	+
B. sphaerocarpa R. Br.	linear	entire	++	1·5–2	2·5–10	2–3	acute	+	small	short	+	+	+
B. telmatiaea A. S. George	linear	entire	++	1–1·3	1·5–4	1·5–2	obtuse	+	small	short	dense	+	+
B. violacea C. Gardner	linear	entire	++	±1·5	1–2	1–2	±obtuse	+	small	short	+	+	(+)
Series *Dryandroideae* Meissner													
B. dryandroides Baxter ex Sweet	linear	lobed	++	7–15	5–17	<1	truncate	–	small	short	dense	+	–


2
3
4
5
B
C
D
E

Abietinae is characterised by very narrow entire leaves with strongly revolute margins and, with the exception of *B. nutans*, nearly isodiametric cuticular cells of the non-stomatiferous surface. *Banksia strahanensis* has slightly wider, less revolute leaves than members of series *Abietinae* and elongate cuticular cells of the non-stomatiferous surface. *Banksia strahanensis* also differs from most taxa of series *Abietinae* in having the stomatiferous area of the cuticle densely and evenly covered with trichome bases and in having no ribs between trichome bases on the cuticle of the non-stomatiferous surface.

Banksia strahanensis is consistent with series *Spicigerae* in all characters except that it shows no evidence of venation on the cuticle of the stomatiferous surface. The cuticles of the stomatiferous surface of all members of section *Oncostylis* have areas of the lamina over veins without stomates (see Fig. 9). This does not occur in *Banksia strahanensis*. *Banksia strahanensis* falls within the range of *B. spinulosa*, particularly var. *spinulosa*, except in this character, in having a longer petiole and the combination of narrow, very revolute leaves without cuticular papillae. Forms of *Banksia spinulosa* with leaves as narrow as those of *B. strahanensis* have abundant cuticular papillae on the non-stomatiferous surface. Of the other members of series *Spicigerae*, *Banksia ericifolia* differs in having shorter, more strongly revolute and narrower leaves with cuticular papillae; *B. brownii* has pinnately lobed leaves and large cuticular cells of the non-stomatiferous surface; *B. occidentalis* has large, almost isodiametric cuticular cells of the non-stomatiferous surface; *B. littoralis* and *B. seminuda* have larger leaves with only recurved margins; *B. tricuspis* has leaves similar to series *Abietinae*; and *B. verticillata* has elliptic leaves and large nearly isodiametric cuticle cells of the non-stomatiferous surface. The fossils are therefore closely related to *Banksia spinulosa* but are sufficiently different to warrant separate specific status.

Section: *Banksia*
Series: *Salicinae* Meissner
Banksia kingii Jordan & Hill, sp. nov.

Diagnosis

Leaves linear-obovate, bifacial, about 1 cm wide and 12 cm long, very thick, with thick revolute margins. Stomatiferous surface with secondary veins diverging at about 60° from the robust midrib, tertiary veins forming a prominent reticulate network. Apex very narrowly emarginate. Petiole 2–3 mm wide, about 2 mm thick, 4–6 mm long. Cuticle of non-stomatiferous surface with cells nearly isodiametric, 4–7-sided, irregularly arranged with porose walls, trichome bases of 1–4 rounded, slightly enlarged cells with thicker cuticle. Cuticle of stomatiferous surface with stomates in irregular-shaped, trichome-filled pits of width exceeding the distance between them and comprising the areoles between the lowest order veins. Cells between pits small, ± rhomboidal, with porose walls and almost all bearing a central trichome.

Location: Late Pleistocene sediments at Melaleuca Inlet, south-west Tasmania.

Holotype: ME-001, stored in the Department of Plant Science, University of Tasmania.

Etymology: In recognition of C. D. King, who found the fossils.

Fig. 2–9. *Banksia strahanensis* and *B. spinulosa*: *2*, holotype of *B. strahanensis* (RPU-381), scale bar = 10 mm; *3*, leaf of *B. spinulosa*, scale bar = 10 mm; *4*, part of a mummified *B. strahanensis* leaf (RPU-023), scale bar = 2 mm; *5*, detail of a *B. spinulosa* leaf, scale bar = 2 mm; *6*, cuticle from non-stomatiferous surface of *B. strahanensis* showing cells, arrows indicate two- and four-celled trichome bases; *7*, cuticle from non-stomatiferous surface of *B. spinulosa*, note dark trichome bases; *8*, cuticle from stomatiferous surface of *B. strahanensis* showing stomatal area with evenly spaced stomates interspersed with single-celled trichome bases and midrib on the right-hand side; *9*, cuticle from stomatiferous surface of *B. spinulosa*, arrow indicates area over vein without stomates. Scale bar for Figs 6–9 = 100 μm.

Specimens Examined

ME-001 to ME-030, stored in the Department of Plant Science, University of Tasmania.

Discussion

Banksia kingii is illustrated in Figs 10, 11, 14 and 16. For comparison *Banksia saxicola* A. S. George is illustrated in Figs 12, 15, 17 and 19, *B. canei* J. H. Willis in Figs 13, 19 and 23 and *B. plagiocarpa* A. S. George in Figs 18 and 22. The robust symmetrical, bilateral leaves with revolute margins and prominent midribs of *Banksia kingii* are typical of subtribe Banksiinae and within this subtribe entire leaves with prominent reticulate venation on the stomatiferous surface occur only in *Banksia* series *Salicinae* (George 1981). The cuticle of *Banksia kingii* is consistent in cell shape, trichome base form and stomatal distribution and form with *Salicinae*. Leaves of similar shape and size to *Banksia kingii* occur in *B. integrifolia* L.f. var *compar* (R. Br.) Bailey, *B. plagiocarpa* and some large-leaved forms of *B. marginata* and *B. canei*. The fossil leaves are more robust than the leaves of any of these taxa, in that they have more sclerified tissue, thicker laminas, cuticles, midribs, margins and petioles. In particular, they are much more robust than the leaves of *Banksia integrifolia* var. *compar* and

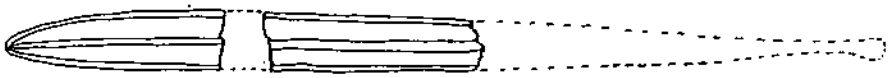


Fig. 10. Reconstruction of *Banksia kingii* leaf. The parts of the diagram in solid outline are derived from the two fragments of ME-001. A portion about 8-mm long connecting the two fragments was poorly preserved and has disintegrated. The leaf base in broken outline has been reconstructed from other fossils, especially ME-002. Scale bar = 10 mm.

any forms of *B. marginata* or *B. canei* that have leaves of similar size to those of *B. kingii*. Only *B. saxicola* and *B. plagiocarpa* have forms which are of similar size and approach the robustness of *B. kingii*. The cuticle of the stomatiferous surface of *Banksia kingii* differs from all these taxa in pit sizes, cell sizes and shapes and/or in the form and distribution of trichome bases. It differs from *B. saxicola* (Fig. 17) only in having larger pits. However, *B. saxicola* has elliptic to obovate leaves (Fig. 12) whereas *B. kingii* has linear obovate leaves (Fig. 10). *Banksia plagiocarpa*, which is similar to *B. kingii* in leaf shape, differs significantly in cuticular characters of the stomatiferous surface in having larger trichome bases placed on small, nearly isodiametric cells and smaller pits (Fig. 18). *Banksia canei* has smaller pits than *B. kingii* and between the pits it has larger cells which rarely have trichome bases (Fig. 19). *Banksia kingii* thus differs from all extant species in both microscopic and macroscopic features and requires specific status. It can, however, be allied to *B. canei* and particularly *B. saxicola* on the basis of shared cuticular characters.

Description of Probable Banksia kingii Infructescences

Infructescence cylindrical, 62 mm long, 46 mm wide including follicles, axis robust (Fig. 26). Styles and perianths absent. Common and floral bracts compactly arranged,

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Figs 11–19. Leaves and cuticles of *Banksia* species. Figs 11–13. Leaves, note the prominent midribs and margins. Scale bar for Figs 11–13 = 10 mm. *11*, Holotype of *B. kingii* (ME-001). A fragment about 8 mm long connecting the two illustrated fragments has been destroyed. *12*, *B. saxicola*. *13*, *B. canei*. *Figs 14 and 15.* Cuticles of non-stomatiferous surfaces. Note the similar-sized nearly isodiametric cells, and the one- to four-celled trichome bases. *14*, *B. kingii*. *15*, *B. saxicola*. Figs 16–18. Cuticles of stomatiferous surfaces. Note the irregularly shaped stomatiferous areas and trichome bases and shapes of cells in the areas between pits. *16*, *B. kingii*. *17*, *B. saxicola*. *18*, *B. plagiocarpa*. *19*, *B. canei*. Scale bars for Figs 14–19 = 100 μm.


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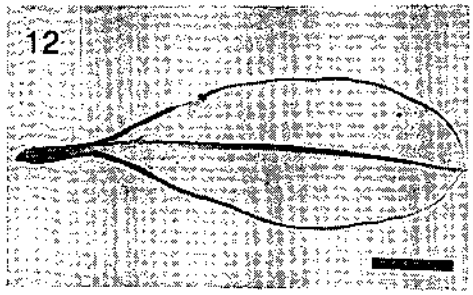
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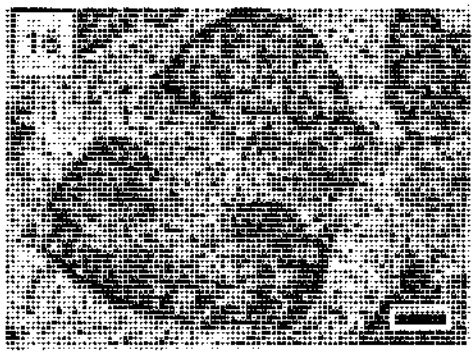
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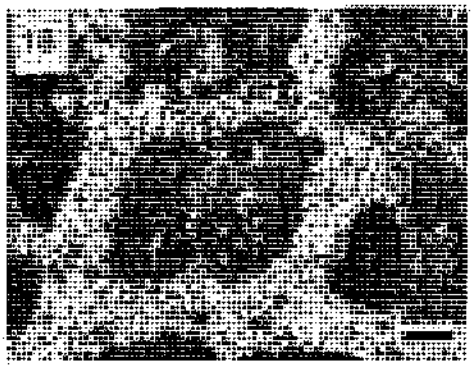
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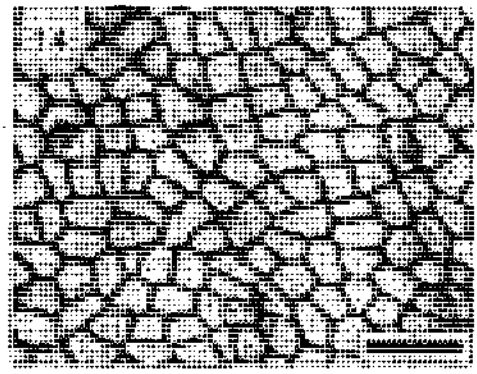
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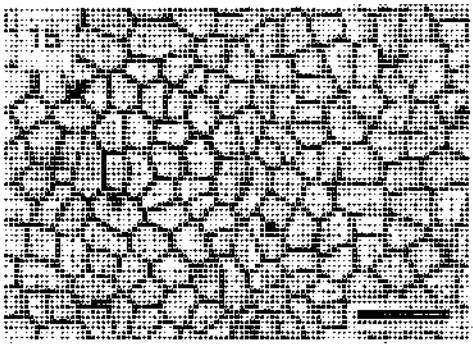
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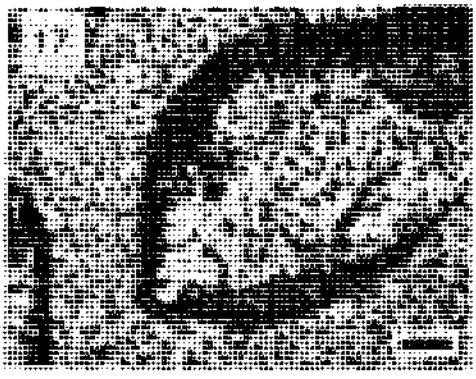
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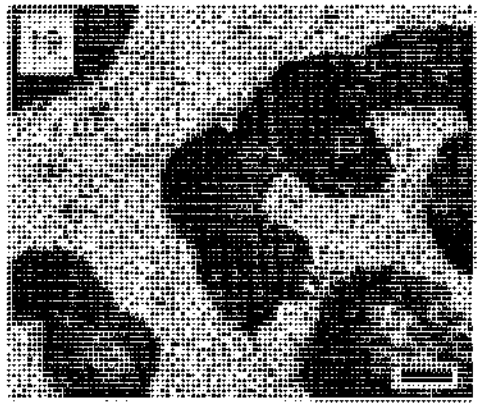
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eroded to an even height of 4 mm, separated by dark brown hairs. Common bracts diamond-shaped, 3 mm × 2 mm. Floral bracts oblong 1·5–2 mm × 1 mm. Follicles oblong in plan view, robust and highly exserted, 11–14 mm wide, 6–7 mm thick, 5–6 mm high, perpendicular to cone axis, sparse and irregularly arranged on cone axis, some remaining closed. Valves semi-elliptic, nearly oblong in section. Ridge wide and obtuse. Separator about 10 mm wide, wings 8 mm × 1·5 mm.

Specimens Examined

ME-031 to ME-033 lodged in the Department of Plant Science, University of Tasmania and several specimens in the possession of C. D. King, Melaleuca Inlet.

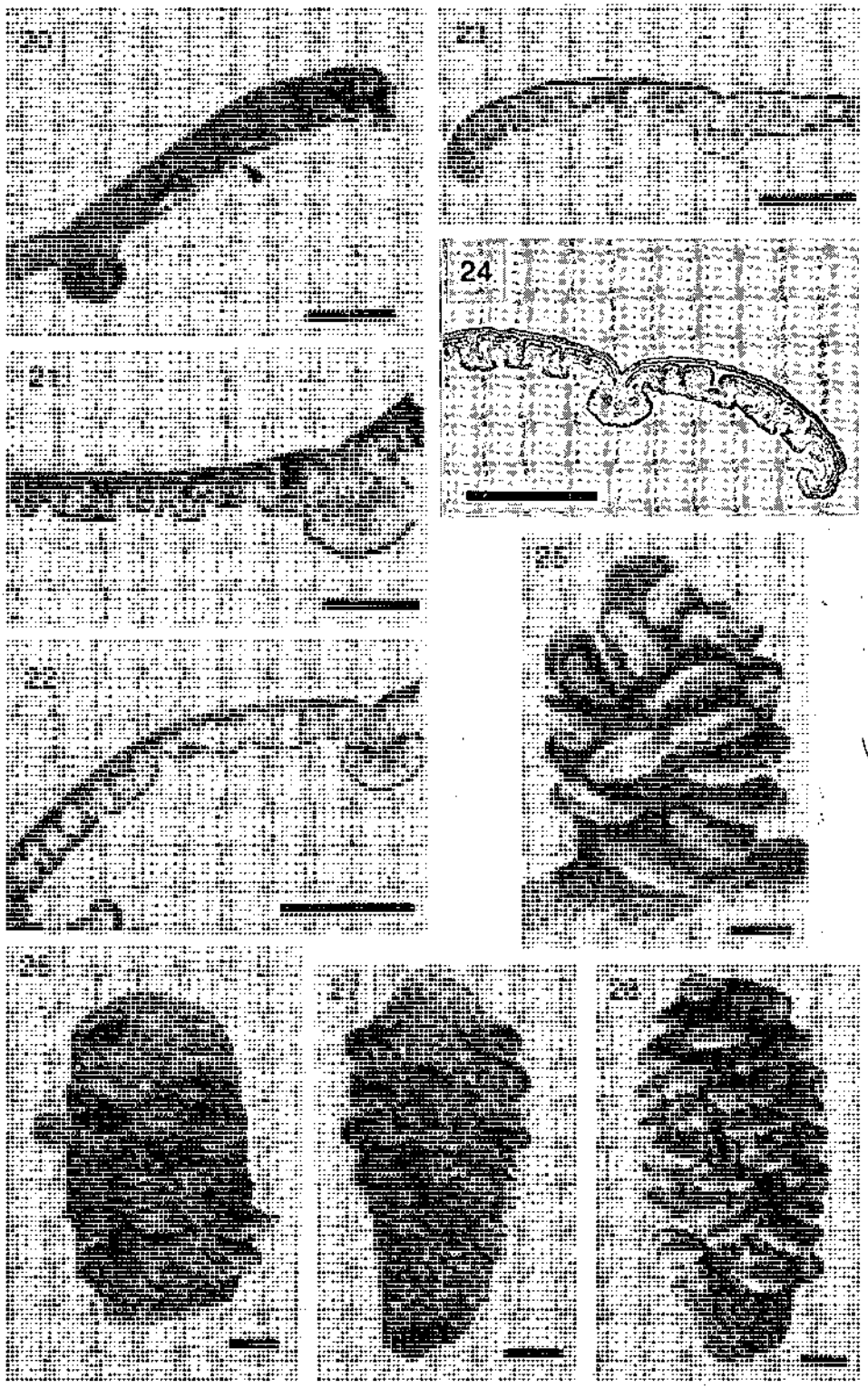
The fossil infructescence (Fig. 26) is morphologically closest to that of *Banksia saxicola* (Fig. 25) but is more robust and has more exserted and robust follicles, which in *B. saxicola* are semi-elliptic in section. The fossil is also related to *Banksia marginata*, *B. canei* and *B. integrifolia*. *Banksia marginata* (Fig. 27) is highly variable, but the fossil infructescence has a more robust axis, early deciduous styles, the follicles are more robust, more exserted, with a thicker ridge and are nearly oblong in plan view and section. Some forms of *B. marginata* appear to have early deciduous styles, i.e. the styles of carpels with unfertilised ovaries are shed soon after the fertilisation of other ovaries, but dissection of the common and floral bracts invariably exposes the lower parts of the styles. Dissecting out the common and floral bracts of the fossil exposes well preserved densely packed hairs with no styles or gaps for styles. The fossil has more exserted, oblong follicles, thicker follicle ridges and narrower separators than *B. canei* (Fig. 28). In *B. canei* the separator has wings nearly as wide as the follicle, whereas those of the fossil are narrow. The fossil has much more robust follicles and infructescence axes than *Banksia integrifolia* which has follicles that are semi-elliptic in section, have narrow ridges and all open at maturity.

These infructescences are consistent with a species closely related to *Banksia saxicola* and *B. canei*, but are sufficiently distinct to warrant specific status. They therefore have similar taxonomic affinities to the *Banksia kingii* leaves. The leaves of *Banksia kingii* and the infructescences were extracted from different lenses at the same site but are of similar ages. Therefore, while there is no direct organic or stratigraphic connection between the two types, the taxonomic similarity and the similarity of age to the *Banksia kingii* leaves seem sufficient for the fruits to be ascribed to *B. kingii*.

Discussion

Banksia strahanensis represents a lineage which is extinct in Tasmania, since no member of section *Oncostylis* occurs there today (Taylor and Hopper 1988). It is unlikely to be ancestral to any extant species of *Banksia* since the absence of veins on the cuticle of the stomatiferous surface does not occur in any extant *Banksia* species and hence seems to be a derived character. Since there is no evidence of the persistence of this species long into the Pleistocene, it is likely that its extinction was due to the climatic and/or physical disruptions of the early Pleistocene glaciations. Its closest relative, *B. spinulosa*, is widespread in south-eastern Australia and occurs on Wilsons Promontory and parts of eastern Victoria (Taylor and Hopper 1988) with cool and wet climates not unlike many parts of Tasmania. It also extends into northern Queens-

Figs 20–28. Leaf sections and infructescences of *Banksia* species. Figs 20–24. Transverse sections of leaves. Note the thicknesses of the laminas, the midribs and the pits. Sections in Figs 21–24 were stained with toluidine blue and sudan III. *20*, *B. kingii* (ME-030), arrow indicates a pit. *21*, *B. saxicola*. *22*, *B. plagiocarpa*. *23*, *B. canei*. *24*, *B. marginata*. Scale bars for Figs 20–24 = 1 mm. Figs 25–28. *Banksia* infructescences. Note the woody exserted follicles interspersed with bracts on a central axis. *25*, *B. saxicola*. *26*, Probable *B. kingii* infructescence. *27*, *B. marginata*, note the narrow infructescence axis. *28*, *B. canei*. Scale bars for Figs 25–28 = 10 mm.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land. Therefore, it is likely that the distribution of *B. spinulosa* is limited by past rather than present climates.

Banksia kingii is related to *B. marginata* which is extant in Tasmania. *Banksia kingii* may be ancestral to *B. marginata* but almost certainly both species were extant at the time of the deposition of the Melaleuca Inlet sediments. *Banksia marginata* is widely distributed in south-eastern Australia, extending from southern Tasmania to northern New South Wales and the Eyre Peninsula in South Australia (Taylor and Hopper 1988) and it is highly unlikely to have radiated into such a large area since speciation later than the time of deposition at Melaleuca. The occurrence of *B. kingii* at Melaleuca is therefore probably evidence of a late Quaternary extinction of a *Banksia* lineage.

The most obvious possible causes of the extinction of *B. kingii* are the climatic disturbances of the last glaciation and/or increased fire frequency due to human activity. There are difficulties with both of these explanations. Extant *Banksia* species are generally highly fire adapted. The *B. kingii* infructescences show some unopened follicles and seeds persistent in other follicles (Fig. 26), which suggests that the seeds are retained for some time on the plant. The retention of seeds is a common fire adaptation in *Banksia* (George 1984). The follicles are also very thick which would allow for some protection of the seed from fire. It is therefore likely that *B. kingii* was adapted to seed release following fire. *Banksia kingii* persisted into the late Pleistocene and must therefore have tolerated the rapid changes of climate and landform of the middle Pleistocene only to be extinguished later. The close relatives of *B. kingii* are *B. saxicola* and *B. canei* which occur in cool to cold, moist areas of Victoria and New South Wales (Taylor and Hopper 1988), mostly on siliceous soils. The leaves of these species approach the robustness of *B. kingii* only on plants growing in exposed, moderately wet, high altitude areas, e.g. *B. saxicola* on the summit of Mt William (1200 m a.s.l.) in the Grampian Range of Victoria and *B. canei* from the top of the Kybean Range of south-eastern New South Wales (1250 m a.s.l.). Both these sites have skeletal siliceous soils. Hence it is likely that *B. kingii* was adapted to harsh and cold but not particularly dry conditions. It is possible that it was a plant of limited tolerance which survived earlier glaciations in small refugia, which were unavailable to it during the last glaciation.

Banksia kingii and *B. strahanensis* are extinct species. They are likely to be from extinct lineages rather than lineages ancestral to extant species. The occurrence of *B. kingii* at Melaleuca Inlet is the only record of an extinct plant species from the Tasmanian late Pleistocene. The occurrence of *B. strahanensis* at Regatta Point is the second macrofossil record of an extinct plant species from the Tasmanian early or middle Pleistocene. Both species are likely to have been adapted to conditions similar to some parts of Tasmania now and have become extinct due to past events. Related species *B. saxicola*, *B. canei* and *B. spinulosa* have distributions that suggest they could now exist in Tasmania, but have been limited alternately by glacial cold and the existence of geographical barriers, particularly Bass Strait.

Acknowledgments

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Late Pleistocene Vegetation and Climate near Melaleuca Inlet, South-western Tasmania

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Abstract

Macrofossils of 27 taxa and microfossils of 47 taxa are identified from a Late Pleistocene deposit at Melaleuca Inlet with a minimum age of 38 800 years. Interpretation of the fossil assemblage suggests that at the time of deposition the climate was cooler than at present and at least as wet. The local vegetation was dominated by wet scrub and sedgeland-heath communities with rainforest and wet sclerophyll forest also present. Species composition was similar to extant vegetation in the region but now-extinct species and possibly communities were present. Charcoal occurs in the sediments and the taxonomic make-up of the assemblage is consistent with the presence of a well established high fire frequency, despite the deposit pre-dating the earliest known human occupation of Tasmania.

Introduction

The ecology of the vegetation of south-western Tasmania cannot be fully understood without knowledge of its Quaternary history. Fossils provide the only direct evidence of this history. Considerable work has been done on Tasmanian Quaternary microfossils, but there has been little detailed macrofossil work. Colhoun *et al.* (1989) and Fitzsimons *et al.* (1990) used preliminary studies of macrofossils and comprehensive microfossil analyses to reconstruct Pleistocene vegetation changes at two western Tasmanian sites. A more detailed study has been made of macrofossils from the Early to Middle Pleistocene Regatta Point sediments (Hill and Macphail 1985; in press).

Plant macrofossils offer a wealth of taxonomic and palaeoenvironmental information. They usually provide more taxonomic information than microfossils, allowing many taxa to be confidently identified to species level in Quaternary deposits. In turn, more precise ecological inferences can be drawn from the species composition of the region at the time of deposition. Macrofossils also provide ecological information in the form of changes in morphology (e.g. leaf macro- and micro-morphology and anatomy may vary within species due to variation in climatic and edaphic conditions). Furthermore, macrofossils are generally more useful than microfossils for inferring past local vegetation types because they are usually dispersed only short distances from their source whereas microfossils tend to be dispersed much further (e.g. Spicer and Wolfe 1987).

The Pleistocene was a period of great climatic upheaval and this undoubtedly resulted in much landform and vegetation change in western Tasmania. The region was glaciated to low altitudes during at least three separate periods in the Pleistocene (Colhoun 1985). Many rainforest species became extinct during the Late Tertiary or Pleistocene, probably resulting in the low diversity of woody plants in extant rainforests (Hill and Macphail 1985; G. J. Jordan, unpublished data).

Jackson (1965) described the extant lowland non-coastal vegetation of south-western Tasmania as a mosaic of hummock sedgeland, shrub moor, wet scrub, wet sclerophyll

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forest, mixed forest and rainforest communities. More recently, the hummock sedgeland and shrub-moor communities have been classified as 'sedgeland-heaths' by Jarman and Crowden (1978). Fire frequencies are now high in sedgeland-heath and wet scrub communities in Tasmania (Jackson 1965; Brown and Podger 1982), although there remains controversy as to whether distribution of these communities is determined principally by fire history or by edaphic features (Jackson 1968; Mount 1979; Brown and Podger 1982). However, there is palynological evidence for the presence of sedgeland-heath communities in western Tasmania as long ago as 17000 B.P. (Macphail and Colhoun 1985) and it has been suggested that wet scrub occurred at Langdon River $\geq$ 43000 B.P. (Colhoun *et al.* 1989). Levels of charcoal similar to those from extant sclerophyll forest were found in the Tullarbardine Dam sediments $\geq$ 43000 B.P. but were associated with an apparently alpine flora (Colhoun and van der Geer 1986). Burnt rainforest taxa dominated one stratum of interglacial sediments at Newton Creek (R. S. Hill, unpublished data). The earliest record of human occupation of Tasmania is about 30000 B.P. (Cosgrove 1989) and therefore, as proposed by Jackson (1965, 1979), Aborigines could have contributed to Late Quaternary vegetation changes by increasing the frequency of fires, resulting in the widespread distribution and abundance of pyrogenic sclerophyll communities. The climatic vicissitudes of the glacial-interglacial cycles would also have contributed to vegetation changes.

In the present study we examine a Pleistocene flora from south-western Tasmania in order to gain a clearer understanding of past vegetation types, climate and fire in the region. Our interpretations are based principally on the macrofossil component of this flora, although a palynological analysis and aspects of the taphonomy of the extant vegetation are also considered.

Materials and Methods

Macrofossils were extracted by either breaking large pieces of sediment open by hand, or by gently macerating them in hot water containing about 5% hydrogen peroxide. Specimens are preserved in alcohol and stored in the Department of Plant Science at the University of Tasmania. To prepare cuticles, leaf fragments were placed in 10% aqueous chromium trioxide and kept warm until all other organic material had oxidised. For scanning electron microscopy, prepared pieces of cuticle were placed on aluminium stubs and sputter coated with gold to a thickness of about 20 nm. Specimens were then studied using a Philips 505 scanning electron microscope operated at 15 kV. For light microscopy, prepared pieces of cuticle were neutralised with 5% ammonia, stained with 1% aqueous safranin O and mounted on slides in phenol glycerine jelly. Dispersed cuticle slides were prepared using the method described in Hill and Macphail (1985).

There is some controversy about the identification of charcoal in fossil deposits, since slow oxidisation of organic material can produce material very similar to charcoal, particularly in Early Tertiary or older sediments (Kemp 1981). It has been suggested that charcoal-like material which is not fire derived will be more prone to chemical oxidisation than charcoal (Harris 1958) and hence boiling material in nitric acid has been used as a test of the source (e.g. Singh *et al.* 1981). The material described as being burnt in this work did not oxidise after boiling in concentrated nitric acid for 1 h. In addition, both carbonised and scarcely altered fossils of the same organs of some taxa occur side by side in the sediments (e.g. *Gleichenia dicarpa* R. Br. pinna fragments). It is therefore very probable that the carbonised fragments in the deposit are the result of fire.

Macrofossil taxa were identified by comparison with herbarium specimens and our collection of cuticle slides and by referral to the taxonomic treatments of Curtis (1963, 1967), Willis (1970), Curtis and Morris (1975), George (1981), Duncan and Isaac (1986) and Wilson and Johnson (1989).

Palynomorphs from the sediments were prepared using the method described in Hill and Macphail (1985) and were examined by M. K. Macphail.

Nomenclature and the current distribution of species follows the taxonomic authorities referred to above and Brown *et al.* (1983). The community types to which the taxa now belong are described according to the classifications of Jackson (1965) and Jarman and Crowden (1978). Species described as occurring in rainforest also occur in mixed forest.

The Fossil Site and Study Area

Sediment containing macrofossils was collected from the late C. D. (Denny) King's tin mine at Melaleuca Inlet, south-western Tasmania (see Fig. 1). The lens was found amongst coarse sand and gravels at a depth of about 2·5 m. The abundance of coarse organic material and the large siliceous particle sizes suggest a high energy depositional environment such as an eddy pool or levee overflow along a fast flowing river. The lens was entirely excavated in mining work about 20 years ago, but all the fossiliferous sediment was piled up and left, without addition of other material (C. D. King, personal communication). Only consolidated sediment was collected for this work, and hence the material is unlikely to be contaminated, except for impregnation by humic water. Wood from these sediments was radiocarbon dated at 38 800 ± 1300 B.P. (SUA 5038) but this should be treated as a minimum age for the reasons discussed by Colhoun (1986).

Brown and Podger (1982) described an area of extant vegetation (Forest Lag) near Melaleuca Inlet which is typical of the region. Sedgeland-heath communities dominated by a mixture of myrtaceous and epacridaceous shrubs and restionaceous and cyperaceous sedges (particularly *Gymnoschoenus sphaerocephalus* (R. Br.) Hook. f.) form the major vegetation cover. Wet scrub communities dominated by *Eucalyptus nitida* Hook. f. with associated species of *Leptospermum*, *Melaleuca* and other shrubs are common. Wet sclerophyll forests in the Melaleuca Inlet region are usually dominated by *E. nitida* with an understorey of small mesophytic trees such as *Pomaderris apetala* Labill. and *Phebalium squameum* (Labill.) Engler. Small cool temperate rainforest patches dominated by *Nothofagus cunninghamii* (Hook.) Oerst. and small mixed forest patches composed of rainforest and wet sclerophyll components also occur.

The climate of the Melaleuca Inlet region is perhumid cool (Gentilli 1972). BIOCLIM (e.g. Busby 1988) estimates of climate are a mean annual precipitation of approximately 2400 mm, a mean annual temperature of 11·5°C, a mean minimum temperature of the coldest month of 4·5°C, a mean maximum temperature of the warmest month of 20°C and rainfall distributed throughout the year, but heaviest in winter.

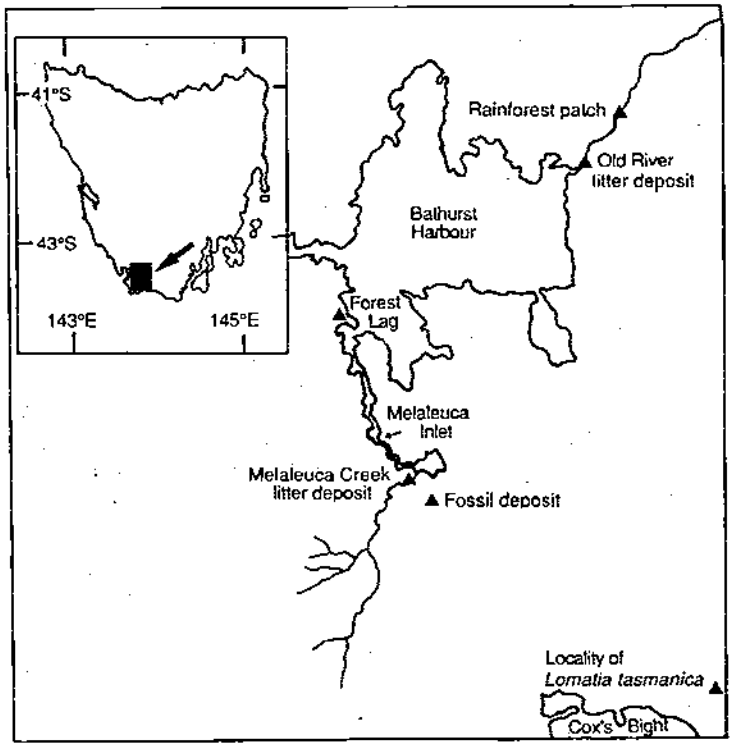


Fig. 1. Location of the Melaleuca Inlet fossil deposit, litter collection sites and other features mentioned in the text.

Taphonomic Analysis

Litter was collected from the Old River and from the bank of Melaleuca Creek (Fig. 1) in order to obtain information about the taphonomy of species in the extant vegetation. The Old River site was on a beach near the river mouth. Vegetation upstream of and around the deposit was dominated by wet scrub and sedgeland-heath, but included wet sclerophyll woodland and a small patch of diverse rainforest about 2 km upstream. The river is of moderate size and contains sections of normally high energy flow adjacent to the section of rainforest. The Melaleuca Creek site was below sections of high energy flow. Vegetation upstream of the site was almost entirely sedgeland-heath with some wet scrub along the creek bank. More than 1900 identifiable macroscopic remains were counted from random subsamples of the litter from each site.

Results

Fossils

Table 1 lists fossils extracted from the deposit. 1342 macrofossils were recovered of which 6 types, making up less than 3% of the total count, were not identified. In addition, over 1300 dispersed cuticle fragments were extracted (5·8% unidentified) and 577 palynomorphs were counted (4% unidentified). At this stage it is not known whether the unidentified fossils belong to extant or extinct taxa.

Table 1. Fossils extracted from Late Pleistocene sediments at Melaleuca Inlet, south-western Tasmania
Figures in the macrofossil column are the percentages of unburnt organs and of burnt organs (in parentheses) of the total macrofossil organ count of 1342. Percentages of dispersed cuticles are based on a total count of 1357. Percentages of palynomorphs are based on a total count of 577. '+' indicates less than 1%, or that the taxon was identified after completion of the count

Taxon and organ	Percentage abundance of: macrofossils	dispersed cuticle	palynomorphs
Dicotyledonous Angiosperms			
Caprifoliaceae			
Sambucus gaudichaudiana DC.			+
Casuarinaceae			19
Allocasuarina zephyrea Wilson & Johnson		23	
Stems with cuticle	45·5 (1·2)		
Cones	0·6		
Compositae			
Cassinia aculeata R. Br. type			+
Cruciferae			+
Cunoniaceae			+ A
Anodopetalum biglandulosum A. Cunn. ex Hook. f.	1·5		
Leaf fragments with cuticle	0·3 (+)		
Bauera rubioides Andr.		49	1
Leaves with cuticle	21·1 (1·2)		
Flower	+		
Elaeocarpaceae			+
Epacridaceae			
Epacris type		0·8	
Epacris heteronema Labill.			1
Leaves with cuticle	3·0 (+)		
Epacris sp. 1 (cf. *E. exserta* R. Br.)			
Leaves	+ (+)		
Epacris sp. 2 (cf. *E. serpyllifolia* R. Br.)			
Leaves	+ (+)		

Table 1 *(continued)*

Taxon and organ	Percentage abundance of: macrofossils	dispersed cuticle	palynomorphs
Epacris/Archeria			
Leaf	(+)		
Capsules	+ (+)		
Monotoca			6
Monotoca glauca (Labill.) Druce			
Fruit	0·4		
Sprengelia type			2
Sprengelia incarnata Sm.			
Leaves with cuticle	1·0		
Eucryphiaceae			+ A
Eucryphia sp.		1·5	
Fagaceae			
Nothofagus cunninghamii (Hook.) Oerst.		0·5	1
Leaves with cuticle	0·4 (+)		
Leguminosae			
Acacia			+
Acacia cf. *mucronata*		+	
Myrtaceae			
Baeckea sp.			
Fruit	+		
Eucalyptus sp.			1
Leptospermum sp.			5
Leptospermum glaucescens S. Schauer		0·3	
Leaves with cuticle	8·0		
Fruit	0·3 (+)		
L. nitidum Hook. f.		0·3	
Leaves with cuticle	+		
Fruit	1·2		
L. scoparium J. R. & G. Forst.		1·2	
Leaves with cuticle	0·3 (+)		
Fruit	1·0		
Melaleuca sp.			5
Melaleuca squamea Labill.		+	
Leaves with cuticle	0·4		
Fruit	0·4		
Melaleuca squarrosa Donn ex Sm.			
Leaves with cuticle	+ (+)		
Fruit	2·0		
Proteaceae			
Agastachys odorata R. Br.		1·4	1
Leaf fragments with cuticle	0·3		
Banksia			3
Banksia kingii Jordan & Hill		2·1	
Leaves with cuticle	3·2		
cf. *Bellendena montana* R. Br.			+
Cenarrhenes			+
Cenarrhenes nitida Labill.		1·2	
Hakea		1·5	
Lomatia cf. *tasmanica* W. M. Curtis		+	
Leaf fragments with cuticle	0·3		
Persoonia			+
Indeterminate Proteaceae			5

Table 1 *(continued)*

Taxon and organ	Percentage abundance of: macrofossils	dispersed cuticle	palynomorphs
Rhamnaceae (not *Pomaderris apetala* Labill.)			+
Rutaceae			+
Thymelaeceae			
Pimelea			+
Winteraceae			
Drimys lanceolata (Poir.) Baill.			+
Monocotyledonous Angiosperms			
Cyperaceae			1
Gahnia grandis (Labill.) S.T. Blake			
Fruit	3·4		
Liliaceae			
Astelia			+
cf. *Blandfordia*			+
cf. Burchardia			+
Milligania			+
Restionaceae			2
Gymnosperms			
Podocarpaceae			
Lagarostrobos franklinii (Hook. f.) Quinn		8	17
Foliage with cuticle	1·6 (+)		
Microcachrys tetragona Hook. f.			+
Microstrobos niphophilus Garden & Johnson			+
Phyllocladus asplenifolius (Labill.) Hook. f.		2·5	12
Phylloclades with cuticle	0·3		
Ferns and Fern Allies			
Gleicheniaceae			10
Gleichenia dicarpa			
Pinna fragments	+ (1·9)		
Other Non-seed Plants			
Cyathea			+
Dicksonia			+
Histiopteris			+
Lycopodium laterale R. Br.			+
Microsorum			+
Indeterminate	3	5·8	4

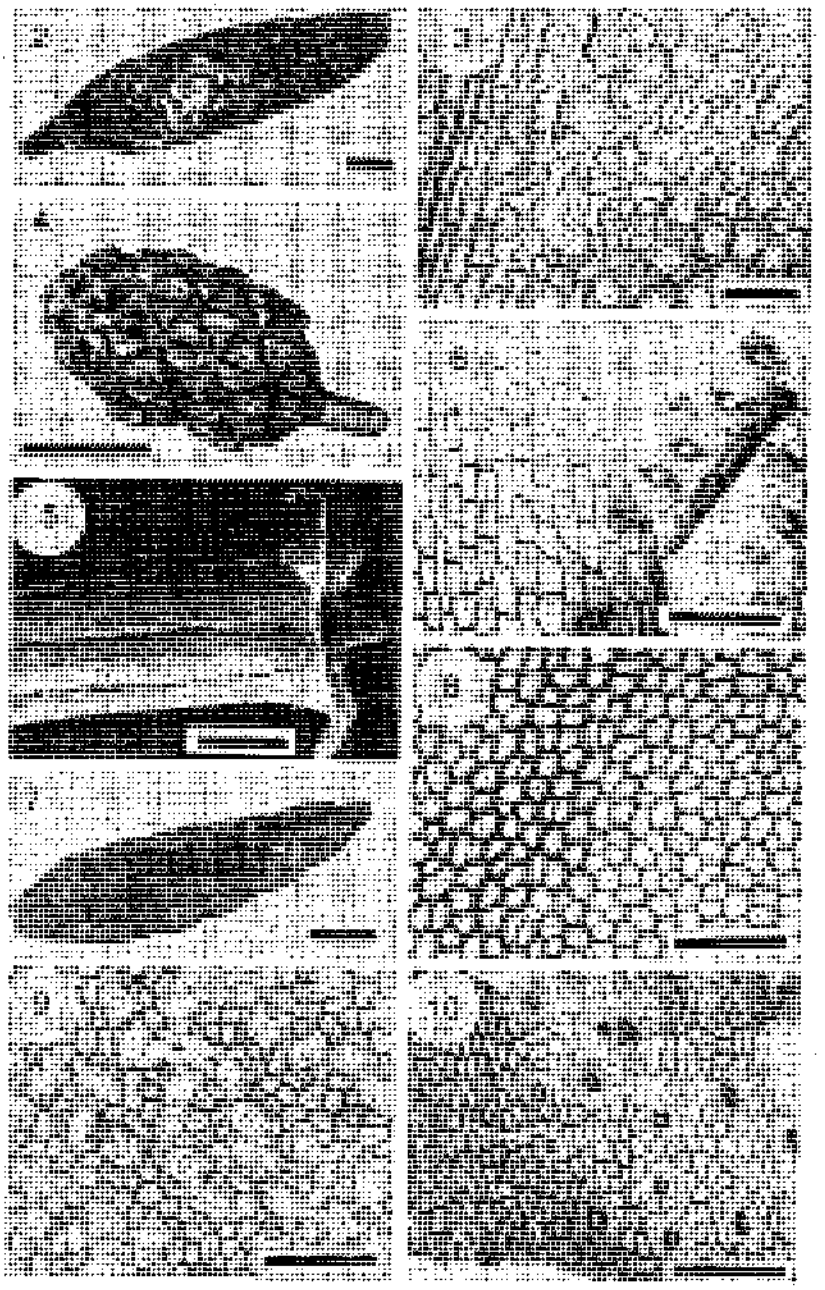
[A] Pollen of either Eucryphiaceae or Cunoniaceae.

Macrofossil taxa, except species previously recorded and well illustrated from western Tasmanian Pleistocene sediments, are shown in Figs 2–41. The taxa and aspects of their current ecology and distribution are listed below in the same order as in Table 1.

(1) *Allocasuarina zephyrea* (Figs 4–6) is now common and widespread in western Tasmania in sedgeland-heath communities, from lowland to lower alpine areas.

(2) *Anodopetalum biglandulosum* (Figs 7–9) is now common in western Tasmanian rainforests and wet scrub and occasionally extends into alpine areas.

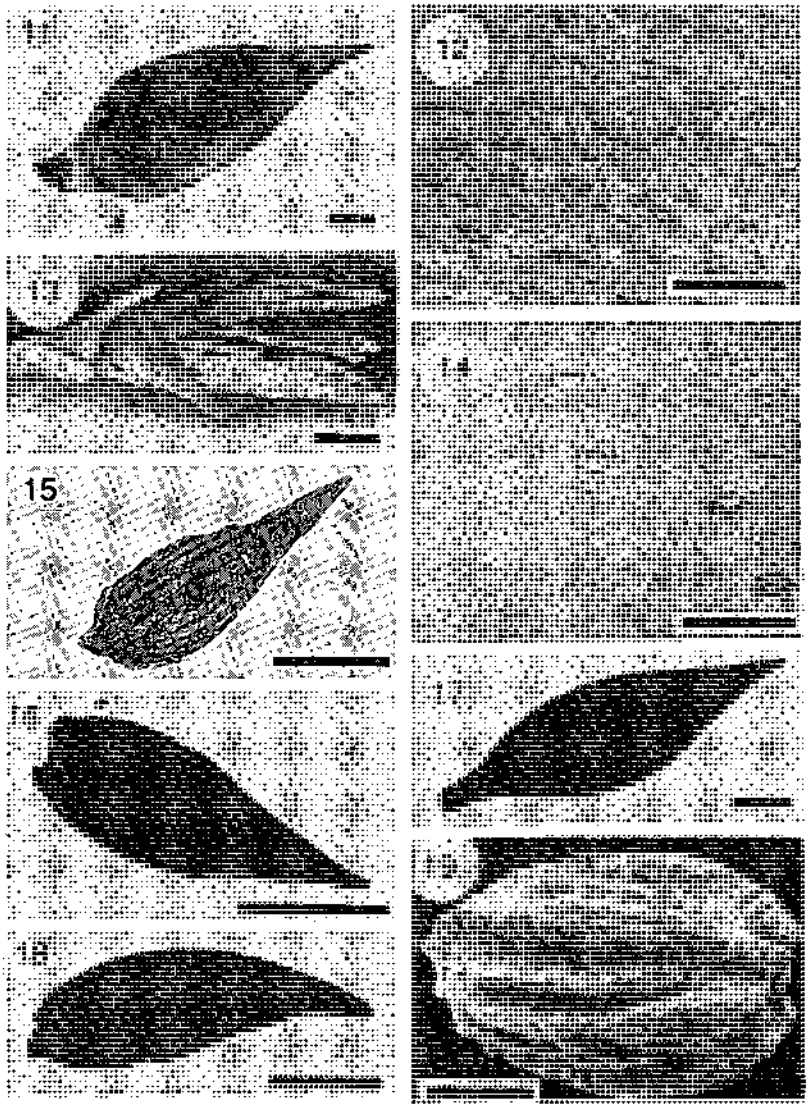
(3) *Bauera rubioides* (Figs 2, 3) is now common and widespread in western Tasmania in sedgeland-heath, scrub and wet sclerophyll forest communities, from lowland to lower alpine areas. It is very common on stream banks.



Figs 2–10. Fossil leaves, cuticles and infructescence. *2, 3, Bauera rubioides* leaf and lower cuticle respectively; *4–6, Allocasuarina zephyrea* infructescence, stem article and cuticle respectively; *7–9, Anodopetalum biglandulosum* leaf, upper and lower cuticles respectively. Note the non-sinuose cuticular cell walls. In *Anodopetalum biglandulosum* this occurs in some high altitude forms. *10*, cuticle of *Acacia* cf. *mucronata*. Scale bars for Figs 2 and 7 = 1 mm, for Figs 3, 6, 8, 9 and 10 = 0·1 mm, for Fig. 4 = 10 mm and for Fig. 5 = 0·5 mm.

(4) *Epacris heteronema* (Figs 11, 12) is now common in sedgeland-heath in south-western Tasmania, from lowland to subalpine areas. The leaves of this species are highly variable within populations and even on single plants. Some of the leaf forms cannot be readily distinguished from other species of *Epacris*, but forms with truncate leaf bases are diagnostic for *E. heteronema*. The sediments contain a wide range of forms typical of modern *E. heteronema* including the diagnostic forms. Fig. 11 shows an intermediate form.

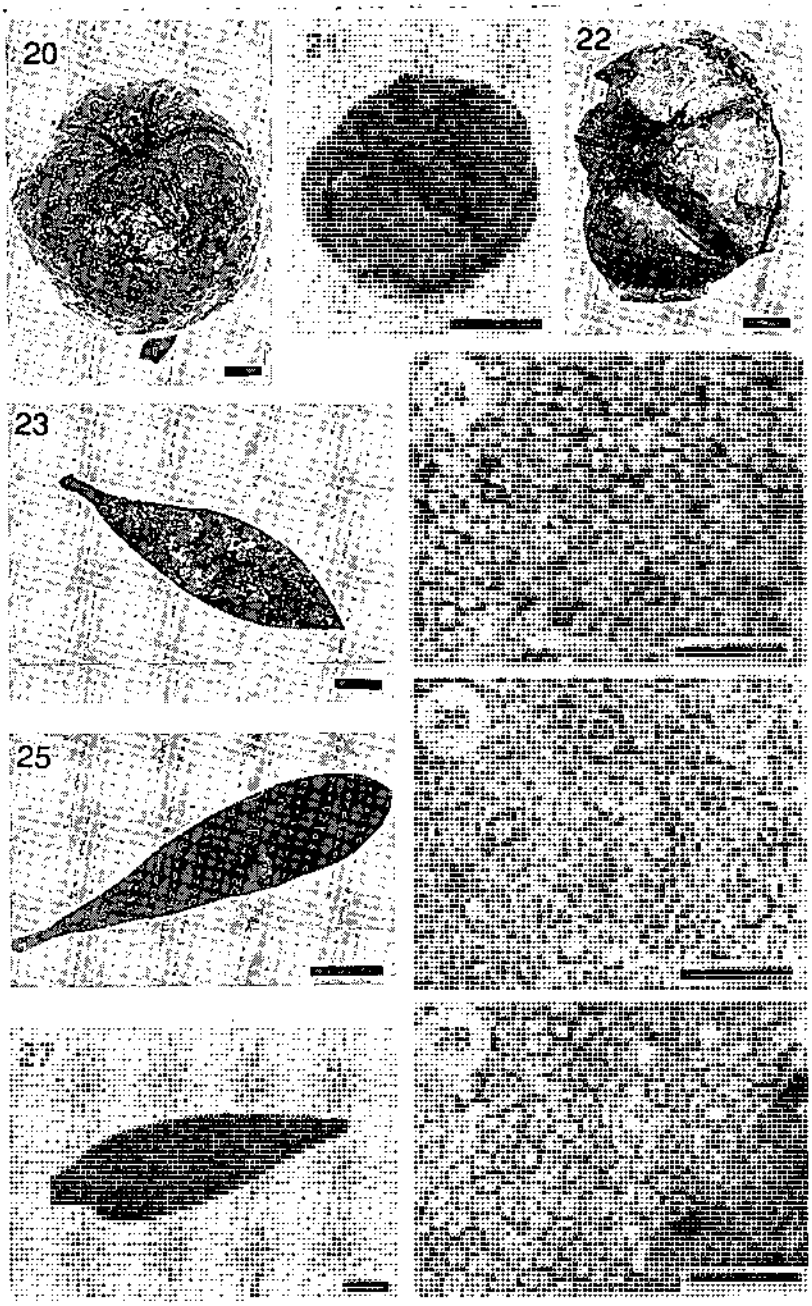
(5) Other *Epacris* leaves (Figs 15–18) cannot be identified to species level. Species having leaves consistent with these now occur widely in Tasmania.



Figs 11–19. Fossil structures of Epacridaceae. *11*, *Epacris heteronema* leaf, the arrow indicates the truncate leaf base; *12*, *Epacris heteronema* lower cuticle; *13*, *14*, *Sprengelia incarnata* shoot tip with flower and cuticle respectively; *15–18*, *Epacris* spp. leaves; *19*, *Monotoca glauca* fruit. Scale bars for Figs 11, 13, 16 and 17 = 1 mm, for Figs 12 and 14 = 0·1 mm and for Figs 15 and 18 = 0·5 mm.

(6) *Monotoca glauca* (Fig. 19) is now widespread and common in scrub and wet sclerophyll forest from lowland to subalpine areas in western Tasmania.

(7) *Sprengelia incarnata* (Figs 13, 14) is now widespread and common in sedgeland-



Figs 20–28. Fossil *Leptospermum* spp. *20, 23, 24, L. nitidum* fruit, leaf and cuticle respectively; *21, 25, 26, L. glaucescens* fruit, leaf and cuticle respectively; *22, 27, 28, L. scoparium* fruit, leaf and cuticle respectively. Scale bars for Figs 20–23, 25 and 27 = 1 mm and for Figs 24, 26 and 28 = 0·1 mm.

heath from lowland to alpine areas. The fossil form is consistent in leaf size with forms other than those occurring in alpine areas.

(8) *Eucryphia lucida* (Labill.) Baill./*E. milliganii* Hook. f. (illustrated in Hill and Macphail 1985) occurs in rainforest from lowland to alpine areas in western Tasmania. Hill (1991*a*) has shown that cuticular characters can be used to distinguish these species. However, the Melaleuca fossils cannot be identified to species level since they are represented by dispersed cuticle fragments lacking sufficient diagnostic features.

(9) *Nothofagus cunninghamii* (illustrated in Hill 1991*b*) is normally the dominant tree species of rainforest in western Tasmania.

(10) *Acacia* cf. *mucronata* is illustrated in Fig. 16. The cuticle of this fossil is consistent with *Acacia mucronata* and is distinct from other extant Tasmanian species, but affinity with other species from mainland Australia cannot be ruled out. *Acacia mucronata* is widespread and abundant in scrub and sclerophyll forest in western Tasmania.

(11) A *Baeckea* species is illustrated in Fig. 33. *Baeckea* species now occur widely in Australia in sclerophyllous heath communities.

(12) *Leptospermum glaucescens* (Figs 21, 25, 26) is now widespread and common in wet scrub and wet sclerophyll forest from lowland to intermediate altitudes in western Tasmania.

(13) *Leptospermum nitidum* (Figs 20, 23, 24) is now very common in lowland *Gymnoschoenus sphaerocephalus* sedgeland-heath communities in western Tasmania.

(14) *Leptospermum scoparium* (Figs 22, 27, 28) is now widespread and common in many habitats including sedgeland-heath and wet scrub from lowland to intermediate altitudes.

(15) *Melaleuca squamea* (Figs 31, 32) is now widespread and common in sedgeland-heath and scrub from lowland to subalpine areas. It also occurs in sclerophyll forest.

(16) *Melaleuca squarrosa* (Figs 29, 30) is now widespread and common in sedgeland-heath and scrub from lowland to subalpine areas. It also occurs in wet sclerophyll forests.

(17) *Agastachys odorata* (Figs 36, 37) is now widespread and common in south-western Tasmania, and occurs in sedgeland-heath, wet scrub, wet sclerophyll forest and rainforest communities from lowland to subalpine areas.

(18) *Banksia kingii* is an extinct species (Jordan and Hill 1991).

(19) *Cenarrhenes nitida* (Fig. 38) is now common in western Tasmania in rainforest and wet sclerophyll forest.

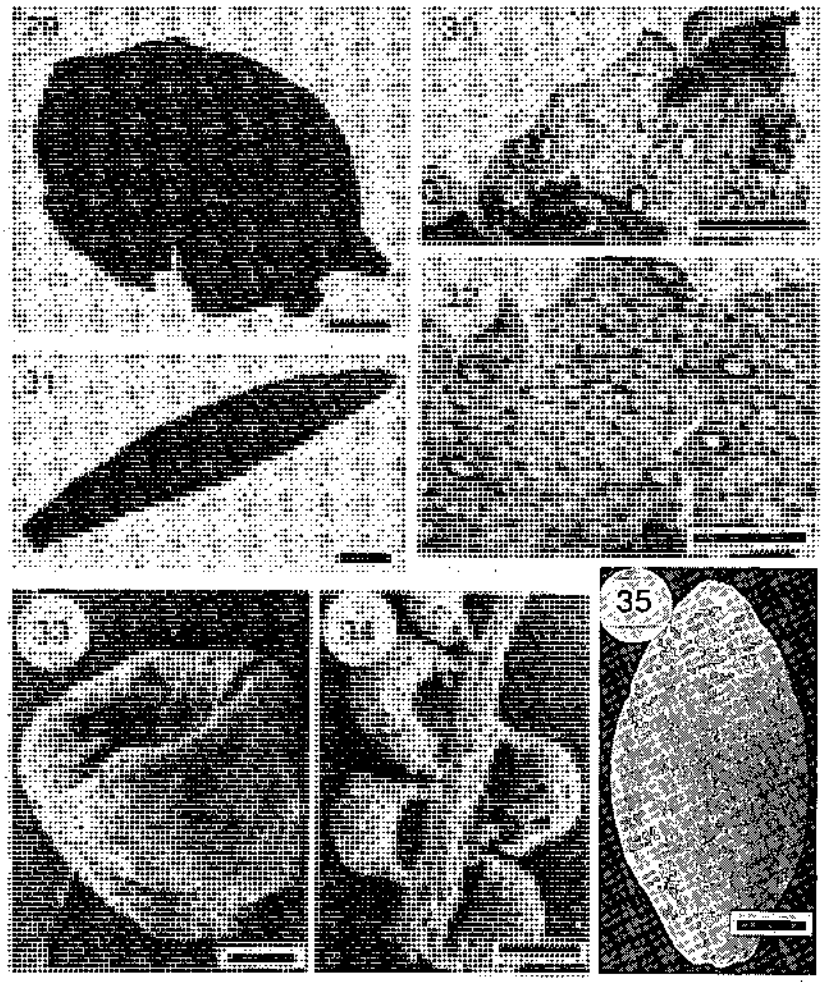
(20) A *Hakea* species (Fig. 39) has cuticle consistent with many species of this large genus. *Hakea* species are common in many sclerophyllous heath communities.

(21) The identification of *Lomatia* cf. *tasmanica* (Figs 40, 41) is based on several well preserved but incomplete leaves. The cuticle morphology and leaf shape of the fossils are entirely consistent with extant *L. tasmanica* (Figs 42, 43) and some extant forms of *L. tinctoria* R. Br., but are quite distinct from all other extant species. *Lomatia tasmanica* only occurs in a small rainforest patch about 12 km from Melaleuca Inlet (Fig. 1). *Lomatia tinctoria* occurs widely in central and eastern Tasmania, but is rare in western Tasmania and is apparently absent from soils derived from Cambrian and Precambrian rock types. These rock types make up the geology of the Melaleuca Inlet region (Williams and Corbett 1977).

(22) *Gahnia grandis* (Fig. 35) is now common in scrub and wet sclerophyll forest communities in Tasmania and is generally associated with fire disturbance.

(23) *Lagarostrobos franklinii* (illustrated by Wells and Hill 1989) now occurs in rainforest in western Tasmania to about 900 m (Peterson 1990), particularly along rivers. It also occurs as seedlings along river banks downstream of adult trees.

(24) *Phyllocladus asplenifolius* (illustrated by Hill 1989) is now widespread and

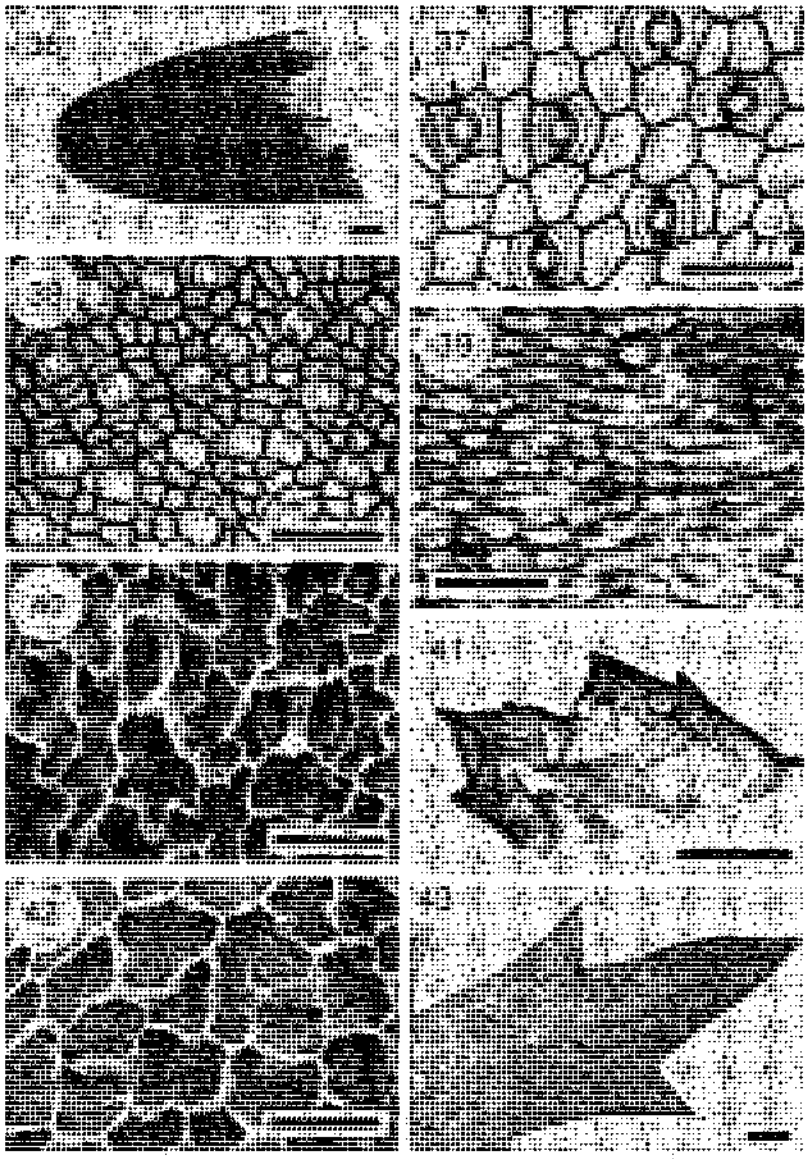


Figs 29–35. Fossil *Melaleuca* spp., *Baeckea* sp., *Gahnia granulis* and [illegible]. *29, 30, Melaleuca squarrosa* leaf and cuticle respectively; *31, 32, Melaleuca squamea* leaf and cuticle respectively; *33, Baeckea* sp. capsule; *34, Gleichenia dicarpa* pinna fragment, the arrows indicate the two sori typical of the species; *35, Gahnia grandis* fruit. Scale bars for Figs 29 and 31 = 1 mm, for Figs 30 and 32 = 0·1 mm and for Figs 33–35 = 0·5 mm.

common in rainforest from lowland to subalpine areas, and occurs in wet sclerophyll forest.

(25) *Gleichenia dicarpa* (Fig. 34) is now widespread and common in sedgeland-heath and wet scrub communities from lowland to intermediate altitudes.

The microfossil assemblage is dominated by Casuarinaceae, *Lagarostrobos franklinii* and *Phyllocladus asplenifolius*, with high proportions of Gleicheniaceae, *Leptospermum* species, *Melaleuca* species, Epacridaceae, Restionaceae and Proteaceae. Many other taxa occur in small amounts. Taxa which do not now occur near Melaleuca Inlet and which are represented in the sediments as palynomorphs but not as macrofossils include *Microstrobos niphophilus* and a single obscured grain of *Microcachrys tetragona*. These species now occur in subalpine to alpine areas of central, western and south-western Tasmania. *Sambucus gaudichaudiana* is now found in lowland areas of northern



Figs 36–43. Fossil and extant Proteaceae. *36, 37,* fossil *Agastachys odorata* leaf fragment and lower cuticle respectively; *38,* fossil *Cenarrhenes nitida* lower cuticle; *39,* fossil *Hakea* sp. cuticle, arrow indicates the ring of cells forming a cone overarching the stomates which identified the genus; *40, 41,* fossil *Lomatia* cf. *tasmanica* lower cuticle and leaf fragment respectively; *42, 43, extant Lomatia tasmanica* lower cuticle and leaf fragment respectively. Scale bars for Figs 36, 41 and 43 = 1 mm, for 37–39 = 0·1 mm and for Figs 40 and 42 = 0·05 mm.

Tasmania and on mainland Australia. *Astelia* occurs in subalpine to alpine areas of Tasmania but also in warmer areas of the world. *Cyathea* is restricted to small lowland patches of northern and eastern Tasmania, but is widespread in wet forests elsewhere in the southern hemisphere.

Taphonomic Analysis

The reconstruction of past vegetation from macrofossils requires caution since the process of fossilisation ensures that fossil assemblages do not mirror exactly the local vegetation at the time of deposition. Differences will be both qualitative and quantitative. Factors favouring fossilisation of one taxon over another were discussed by Birks and Birks (1980) and Ferguson (1985) and include the type of leaf form, the degree of sclerophylly, the content of secondary substances and the buoyancy of the plant part. Some taxa are highly unlikely to fossilise in high energy systems due to their habit (e.g. ground covering herbs), or due to their structure (e.g. those with fragile leaves or leaves which are quickly attacked by insects or fungi after abscission).

Fig. 44 shows relative proportions of the macrofossils in the sediments and of major species occurring in litter from the Old River and Melaleuca Creek sites. Major differences between the representation of species in the litter and in surrounding vegetation are apparent. These differences can be used to infer the relative likelihood of fossilisation of different taxa, and in turn are important for interpreting the make-up of the macrofossil assemblage.

Eucalyptus nitida, Allocasuarina zephyrea, Gleichenia dicarpa, the sedge families Restionaceae and Cyperaceae and other herbs are all prominent in the vegetation around and upstream of the two litter collection sites, but are rare or absent in the litter and are thus under-represented. *Eucalyptus* species were also under-represented in litter samples elsewhere in Tasmania (Hill and Gibson 1986; Carpenter and Horwitz 1988). This is probably because their leaves are poorly dispersed and are apparently susceptible to rapid biological breakdown. The under-representation of *Allocasuarina zephyrea* is explained by the fact that although these shrubs have robust foliage and are quite common in the surrounding vegetation, they rarely occur along streams. Members of Restionaceae and Cyperaceae are very abundant in all vegetation types in the region except rainforest, but organs of these families were not recognised in the litter samples. These taxa and *Gleichenia dicarpa* exhibit a low growing habit in the region and have quite wiry or rigid foliage which is unlikely to become detached. Also, the cuticle of these plants is usually fragile.

Nothofagus cunninghamii, Lagarostrobos franklinii, Eucryphia lucida and *Phyllocladus aspleniifolius* each make up between 0·9 and 3·5% of the Old River sample but are locally rare or absent and are therefore considered to be over-represented in this sample. The nearest source of *N. cunninghamii* and *E. lucida*, and the nearest site where *L. franklinii* and *P. aspleniifolius* are common, is a small rainforest patch about 2 km upstream of the collection site. *Phyllocladus aspleniifolius* is also over-represented in the Melaleuca Creek litter as although it makes up only about 0·8%, it does not occur for at least 1 km upstream. Phylloclades would therefore be expected to be very rare or absent from the litter, given non-preferential deposition. Hill and Gibson (1986) showed that *N. cunninghamii* was over-represented in litter on the floor of a small subalpine lake, and Carpenter and Horwitz (1988) suggested that *N. cunninghamii, P. aspleniifolius* and *E. lucida* are all likely to be over-represented in fossil assemblages because of their general abundance along water courses, their tree habit and their possession of robust foliage. Similarly, we have observed that shoots of *Lagarostrobos franklinii* are generally common in riverine litter for a substantial distance downstream of even a small source. Therefore, it is likely that all of these species will be fossilised preferentially over most other common taxa extant in the Melaleuca Inlet region.

Some non-rainforest taxa are well represented in the litter. *Bauera rubioides, Epacris heteronema, Sprengelia incarnata*, three species of *Leptospermum* and two of *Melaleuca* are all common in the local vegetation, but make up very high proportions of the litter (Fig. 44) and are probably over-represented. These species have small sclerophyllous

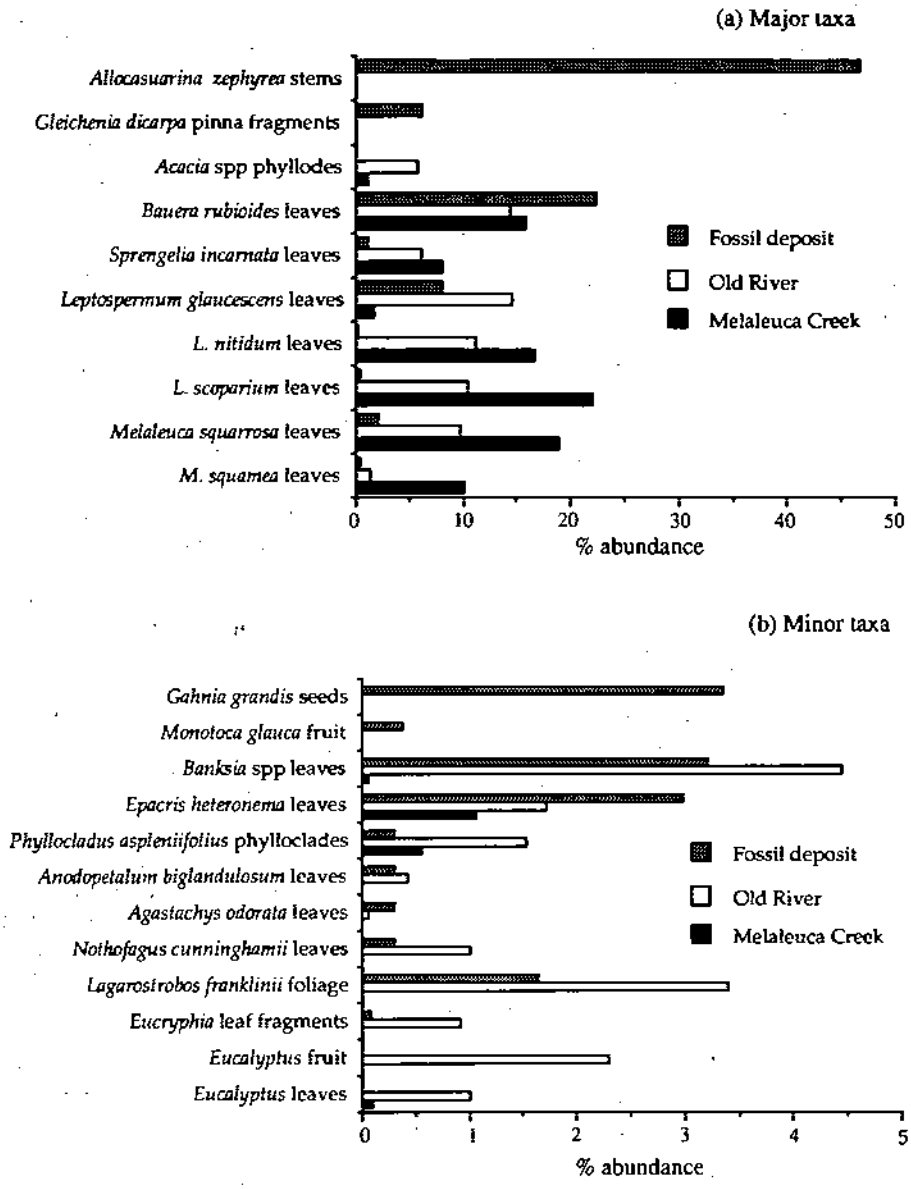


Fig. 44. Comparison of the relative abundances of selected taxa in the Melaleuca Inlet sediments with abundances in two riverine litter samples representing extant vegetation of two nearby localities: along the Old River, and along Melaleuca Creek. (*a*) Taxa which each make up more than 5% of at least one of the samples. (*b*) A subset of those taxa which each make up less than 5% of any of the samples.

leaves and with the exception of the *Melaleuca* species, which have a particularly fragile cuticle, all seem likely to have a high potential for fossilisation.

Reproductive structures may be under-represented in the litter because the samples were taken in summer and the sites are certain to have been flushed by winter and spring flooding. Their under-representation in the litter samples therefore does not reflect on their ability to be fossilised except in that there may be seasonal variation.

Burnt plant organs may be more likely to be preserved than unburnt organs since they are less likely to be degraded biologically. There were no burnt organs in the litter but this is most likely due to the recent absence of nearby fire.

Discussion

Climate

Following are several features that suggest that the climate at Melaleuca Inlet at the time of deposition is likely to have been as cool as or cooler than it is now.

(1) The present day distributions of all extant species listed, except *Sambucus gaudichaudiana*, are consistent with such a climate and there are several features which suggest a cooler climate than at present.

(2) The extinct species *Banksia kingii* shows affinities with *B. saxicola* A. S. George and *B. canei* J. H. Willis of Victoria and New South Wales (Jordan and Hill 1991). It has a very thick lamina, cuticle and petiole. These traits are positively correlated with altitude in *Banksia* series *Salicinae* but are more extreme in the specimens from Melaleuca than in any specimens of this series examined (G. J. Jordan, unpublished data). In these traits the fossil most closely resembles high altitude forms of these species, e.g. *B. saxicola* from Mt Williams (about 1200 m) in the Grampians in Victoria, and *B. canei* from the Kybean Range (about 1250 m) in N. S. W. Leaves of *Banksia marginata* from Mt Williams and similar habitats have much thicker cuticle, lamina and petiole than leaves of populations in lowland south-western Tasmania, and hence these changes in morphology are likely to have resulted from the effects of decreased temperature. Increased wind abrasion, high insolation or periodic desiccation are less likely to be the causes of these morphological traits since the Melaleuca Inlet site was lowland and apparently at least as wet as it is now.

(3) The leaf size and cuticle morphology of *Anodopetalum biglandulosum* from the deposit is outside the range of present day low altitude forms of the species, and is consistent with some high altitude forms (e.g. from Mt Read, 1140 m). The leaves of other taxa also tend to be smaller than those of the present day members of these taxa currently in the same area. This, however, may be a preservational artefact, since small leaves are probably more likely to survive the processes of preservation as fossils.

(4) The presence of currently alpine taxa such as *Microstrobos niphophilus* and a species of *Astelia* may be significant, although these taxa only occur as pollen and may therefore have reached the sediments through long-distance dispersal.

The present distributions of the identified taxa are consistent with a climate as wet as or wetter than the current one at Melaleuca Inlet. In particular, many of the species, including *Agastachys odorata, Epacris heteronema, Eucryphia* species and *Lagarostrobos franklinii* are now restricted to the wetter parts of Tasmania.

There is independent geological evidence which strongly suggests the presence of very high levels of precipitation. The lens was found between facies of river gravels and stones, indicative of much fluvial activity. As the regional topography in the Pleistocene would have been almost identical to now, it is assumed that the deposition of such sediments in a possible braided river situation was a consequence of very high rainfall.

Vegetation Reconstruction

Vegetation reconstructions are based on extant vegetation types and the ecology of the extant taxa of closest affinity to the fossils. Where leaf fossils can be confidently identified to species and are morphologically similar to extant forms it is assumed that they have similar ecological tolerances.

The array of macrofossil species in the Melaleuca Inlet sediments suggests that more

than one vegetation type contributed to the assemblage. The lens appears to have been deposited in a river, and therefore may contain plant organs from riparian vegetation some distance upstream, thus explaining an input by more than one vegetation type. The deposit contains elements now generally found in rainforest (*Nothofagus cunninghamii, Eucryphia lucida* and *Anodopetalum biglandulosum*), in sclerophyll forest and scrub (*Leptospermum glaucescens, Monotoca glauca* and *Gahnia grandis*) and in sedgeland-heath (*Leptospermum nitidum, Epacris heteronema* and *Sprengelia incarnata*). Other species frequently occur in more than one of these vegetation types.

The proportions of taxa in the fossil deposit are sufficiently similar to those from the Old River litter sample to allow us to use this site for comparison. Both contain large amounts of *Bauera rubioides* and *Leptospermum glaucescens* and have comparable amounts of *Melaleuca* species and *L. scoparium*. These together suggest a dominance of wet scrub, at least along the river banks. The two sites also show comparable amounts of the rainforest species *Nothofagus cunninghamii, Phyllocladus aspleniifolius* and *Lagarostrobos franklinii*. The rainforest is distant from the Old River site and we infer that rainforest was either distant from the fossil site or it comprised only a small part of the local vegetation, particularly since these species tend to be over-represented in sedimentary environments.

The palynological evidence is consistent with the conclusion from macrofossil evidence that sedgeland-heath and wet scrub were common in the region. In particular, the sedge families (Cyperaceae and Restionaceae) and sclerophyllous heath taxa (*Melaleuca, Leptospermum*, Epacridaceae and Proteaceae) are all common, with moderate levels of *Eucalyptus* pollen also present. There are no clear indications for the presence of wet sclerophyll forest, although some palynomorphs are consistent with the presence of small regions of this community type (e.g. *Dicksonia, Cyathea* and *Cassinia aculeata* type). Pollen of the rainforest species *Lagarostrobos franklinii* and *Phyllocladus aspleniifolius* is abundant, but it is significant that pollen of the major extant rainforest species, *Nothofagus cunninghamii*, is not common. These pollen types are characteristically over-represented (e.g. Hill and Macphail 1985). Therefore, we conclude that a form of rainforest was likely to have been present but not dominant in the region. The palynomorph taxa represented are in general typical of extant lowland vegetation of western Tasmania, with the exception of the low percentage of some alpine taxa (*Microstrobos niphophilus, Microcachrys tetragona* and *Astelia* species) and of *Sambucus gaudichaudiana* and *Cyathea*.

Macrofossil and microfossil analyses of the Melaleuca Inlet sediments therefore provide independent lines of evidence consistent with a local and regional vegetation dominated by scrub and sedgeland-heath, with some rainforest.

There is evidence of only one total extinction, that of *Banksia kingii*, and of few regional extinctions, including *Cyathea* and *Sambucus gaudichaudiana*. However, there are significant differences between the inferred fossil vegetation and extant vegetation. *Banksia marginata* Cav. is common in the region today but is not present in the deposit, whereas the extinct *B. kingii* is common. The highly sclerophyllous leaves of *B. marginata*, its presence in the two litter samples and the abundance of *Banksia*-like species in many Tertiary fossil deposits (Cookson and Duigan 1950; Hill and Christophel 1988) all suggest that *B. marginata* is likely to fossilise well. Its absence from the deposit indicates that it was rare or absent in streambank vegetation at the time of deposition. The presence of *Lomatia* cf. *tasmanica* in the sediments requires that the range of *L. tasmanica* was much greater than, or different to its current range, that the range and ecological preferences of *L. tinctoria* were different to its current range and preferences, or that a closely related species of *Lomatia* has become extinct.

There is also evidence for the existence of now extinct plant communities. In particular, *Allocasuarina zephyrea* is the dominant macrofossil taxon in the deposit, but was not

found in extant litter samples and is now uncommon along riverbanks in south-western Tasmania. This suggests that, at the time of deposition of the Melaleuca sediments, *A. zephyrea* formed a major component of the vegetation of the area at least along riverbanks. The combination of very high levels of *Phyllocladus asplenifolius, Lagarostrobos franklinii* and Casuarinaceae pollen with low levels of *Nothofagus cunninghamii* pollen is unknown from the Late Pleistocene and is very unlikely to occur in modern vegetation. *Phyllocladus asplenifolius* and *L. franklinii* now rarely, if ever, co-dominate vegetation without *N. cunninghamii* being abundant, at least nearby, and never are co-dominant with Casuarinaceae. Macrofossils and microfossils from most other known Pleistocene macrofossil localities in western Tasmania also show high proportions of *Allocasuarina* associated with high levels of some combination of *L. franklinii, N. cunninghamii* and/or *P. asplenifolius*. These sites are Langdon River (≥ 43 000 B.P.) (Colhoun *et al.* 1989), the King River Valley (Early to Middle Pleistocene) (Fitzsimons *et al.* 1990), Newton Ck (R. S. Hill, unpublished data) and Regatta Point (Early to Middle Pleistocene) (Hill and Macphail 1985, in press: G. J. Jordan, unpublished data). It is therefore likely that *Allocasuarina* formed associations with species that are now typical of rainforest, and these associations are unlike any now known. The absence of *Eucalyptus* macrofossils and low representation of pollen is also significant as it indicates that the genus was not as common in the region as it is today. Its pollen is well represented in modern samples from a variety of vegetation types (Colhoun and van der Geer 1986) and can be transported over long distances (e.g. Hill and Macphail 1985).

The role of fire in the evolution and current structure of Tasmanian vegetation is the subject of continuing debate. The Melaleuca sediments contain evidence for the occurrence of local fire in the form of burnt plant organs, and the assemblage is composed of numerous elements which today are regarded as dominants of pyrogenic communities (Jackson 1979). Further, there are burnt remains of rainforest species such as *Lagarostrobos franklinii*, which is recognised as being fire sensitive (Gibson 1986). It is possible that the macrofossil assemblage reflects the scenario of many modern fires in the south-west, where the perimeters of patches of rainforest are burnt. The presence of fire and the abundance of sedgeland-heath and wet scrub suggested by the Melaleuca Inlet fossils is of considerable interest. If the deposit was laid down before human occupation of Tasmania, lightning must have been the ignition source for the fires, in spite of the wet climate apparently present at the time. Either low fire frequency regimes maintained by lightning were sufficient to maintain sedgelaud-heath and wet scrub forest communities, or lightning provided much higher fire frequencies than is often considered possible. Another possibility is that Aborigines may have been present in Tasmania early enough to create well established fire dependent communities at the time of deposition. Alternatively, it is possible that fires were very infrequent and that the presence of these sclerophyllous communities was a direct consequence of extremely oligotrophic conditions, which may have been exacerbated by the leaching effects of very high rainfalls.

Further macrofossil oriented research on Pleistocene floras is required before the nature of Tasmanian vegetation during this period of profound environmental change can be understood more fully. These studies are likely to contribute much to our knowledge of the ecology of modern vegetation associations and the effects of climatic change.

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